

Short Communications

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American Robin *Seet* Calls: Aerial Alarm or a Contact Call?

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ABSTRACT.—The literature regarding the *seet* call of the American Robin (*Turdus migratorius*) is unclear as anecdotal accounts indicate it is an aerial alarm. A more recent, comprehensive account indicates it is most likely a contact call. We examined the meaning of *seet* calls through observations and a playback experiment, both of which support the aerial alarm function of the call. Robins only gave *seet* calls to aerial predators and many engaged in skygazing, a behavior previously unreported for robins. Robins engaged in three anti-predator behaviors, skygazing, alert, and scanning for significantly more time after hearing an alarm compared to hearing a control. American Robins, like many other birds, probably evolved this call to avoid detection by aerial predators and to warn conspecifics. Received 14 July 2008. Accepted 14 December 2008.

Birds use a variety of calls to communicate and can readily comprehend and discriminate between calls in their repertoire. However, it often takes years for scientists to fully understand the context and meaning of many calls. The study of avian communication has evolved from largely observational accounts to hypothesis-driven experimentation, often with aid of technology, which has allowed scientists to discern the meaning of many birds' calls (Baptista and Gaunt 1994). Alarm calls may be particularly important communications, as they may allow birds to warn conspecifics and escape predation, and potentially have an immediate effect on fitness (Klump and Shalter 1984). Many birds have alarm calls and, in some species, different kinds of alarms are given for different types of threats (Marler 2004). Some species give distinctive alarms for ground and aerial predators, a refinement that allows conspecifics to gain much more information from the alarm and

respond appropriately for a specific kind of threat (Evans et al. 1993, Evans 2002). For example, Steller's Jay (*Cyanocitta stelleri*) give a *wah* call when mobbing ground predators and a high-pitched call when hawks are seen (Hope 1980), both of which elicit a different response. We investigated whether the American Robin (*Turdus migratorius*) has a distinctive aerial alarm call given for aerial predators and examined conspecifics' response to that call.

Previous research on robin alarm calls focused on those given in response to terrestrial predators, and these calls have been clearly characterized (Shedd 1982, Gottfried et al. 1985). Robins give two types of terrestrial alarm calls, *yeeeps* and *chucks*. However, robins also have numerous aerial predators with accipiters (Cooper's Hawk [*Accipiter cooperii*] and Sharp-shinned Hawk [*A. striatus*]) being particularly important predators (Roth and Lima 2003, Roth et al. 2006) and, accordingly, an aerial alarm might provide a strong selective advantage. Currently there are conflicting reports in the literature concerning whether or not robins have an aerial alarm. Two anecdotal reports from the 1950's suggested that robins give a *seet* call in the presence of aerial predators and that robins become "rigid" when they hear that call (Jackson 1952, Hailman 1959). The *seet* call is higher pitched and longer in duration than other alarm calls in the robin's repertoire (Fig. 1) and it sounds similar to the call of Cedar Waxwings (*Bombicilla cedrorum*); robins often have bouts of *seet* calls, during which they repeatedly give this vocalization. Two later studies assumed the robin *seet* call was an aerial alarm and used it in investigations of hawks' perception of alarm calls (Brown 1982, Jones and Hill 2001). A recent review of robin behavior and ecology by Sallabanks and James (1999) suggested this call might be used as a contact call between males and females, and between par-

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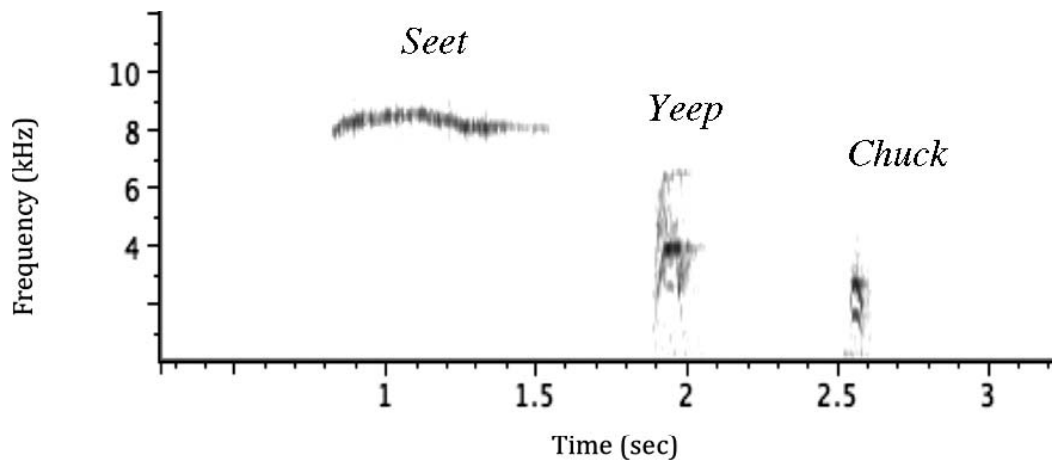


FIG. 1. Spectrogram of American Robin alarm calls.

ents and young; however, they did not mention its possible use as an aerial alarm.

Our goal was to clarify the meaning of the American Robin *seet* call and conspecifics' responses to the call. We first examined the context of the call, recording whether we could see a terrestrial or aerial predator when a robin gave *seet* calls, and then recorded the calls for description and analysis. We also noted the behavior of conspecifics in response to the calls. Finally, we compared the responses of robins to recorded calls and a control of white-noise in a playback experiment.

METHODS

We conducted our study from 25 May to 25 November 2006 at two public parks in Louisville, Kentucky: Joe Creason Park (27.5 ha; 38° 12' N, 85° 42' W) and George Rogers Clark Park (18.6 ha; 38° 12' N, 85° 42' W). Both parks contain forested patches and open grassy areas with scattered trees. We recorded six bouts of *seet* calls during spring 2006 using a Sennheiser ME 62 directional microphone connected to a Sony TCM-5000 EV recorder. Recordings were made within 3 m of the vocalizing robin and, in all instances, a raptor (*Accipiter* spp.) was seen in the area immediately prior to or during recording. We analyzed these calls using Raven bioacoustic software (Cornell Laboratory of Ornithology 2003) and recorded the following: length of the calling bout, number of calls within a bout, inter-call interval, and call rate (number

of calls/min). We also calculated the average duration, and minimum and maximum frequencies of a single *seet* call.

We collected data on the occurrences of *seet* calls on 31 days between 26 May and 21 September 2006 to test if *seet* calls were given solely in the presence of aerial predators. We noted when we heard a *seet* call and recorded whether we observed a raptor or terrestrial predator when the alarm was given. We compared the proportion of calls given in the presence of aerial predators versus terrestrial predators with Chi-square. We also noted during this observational study when robins displayed one anti-predator behavior not previously reported in this species, skygazing. Skygazing behavior was defined by the following postural change: robin froze, squatted low to the ground with its neck bent towards its back and beak pointing skyward. Individuals hearing *seet* calls as well as individuals giving *seet* calls displayed this behavior.

We conducted a short playback experiment in which we played recorded *seet* calls to 10 adult robins and a control (white noise) to an additional 10 adult robins while they were foraging on the ground. We performed these playbacks only when no terrestrial or aerial predators were visible in the area and when no robins had been giving any alarm calls for at least 30 min. The *seet* call playback consisted of three *seet* calls played over 15 sec, which represented a short bout and a conservative test of robins' responsiveness to this

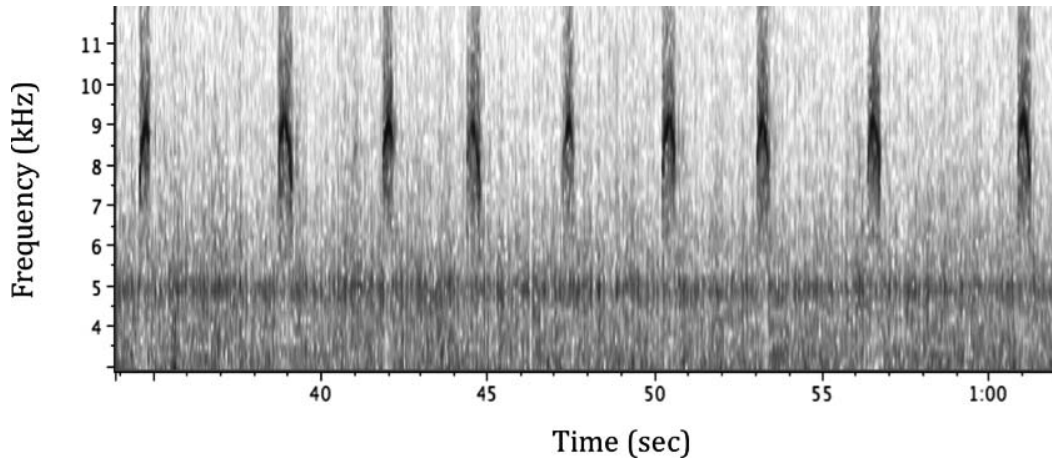


FIG. 2. Spectrogram of American Robin *seet* call bout.

call. We also recorded white-noise, broad band noise at a constant frequency, for 15 sec as a control. We observed robins for 2 min after playing either white noise or the *seet* calls. We noted whether or not the focal bird stopped foraging during these observations and whether the bird performed any of three anti-predator behaviors. These behaviors included standing alert, scanning, and skygazing. Robins standing alert froze in an erect position; scanning birds also stood in place but turned their heads rapidly from left to right, appearing to scan the area. We performed a Chi-square test to compare the proportion of robins that stopped foraging after hearing a *seet* call versus after hearing white-noise. We used MANOVA to compare the robins' behaviors after playbacks between the two treatments. SAS (SAS Institute Inc. 2003) was used for all statistical tests and data are reported as means \pm SE.

RESULTS

The call bouts of American Robins giving *seets* lasted on average 186 ± 49.9 sec (range 23–315), and the average number of calls given within a bout was 38.8 ± 12.3 . The interval between calls was 5.5 ± 1.1 sec (range 1–33) and, on average, robins gave 11.4 ± 2.9 *seet* calls/min. Individual *seet* calls lasted <1 sec (0.424 ± 0.010 , $n = 130$) and had a minimum frequency of 7306.6 ± 38.5 Hz and a maximum frequency of 9012.3 ± 67.6 Hz ($n = 130$; Fig. 2).

We heard robin *seet* calls on 29 of 31 observation days. We observed solitary robins and those in flocks emitting *seet* calls. However, on most occasions we observed calling birds after the initial vocalizations and were unable to tell if the bird was alone at the time the alarm was initially given. We saw an aerial predator (accipiter hawk) on 16 of the 29 occasions. There were many terrestrial predators at the parks where we conducted our study, but we did not hear robins give the *seet* call in response to any terrestrial predator ($\chi^2 = 22.0952$, $P < 0.0001$). We also saw robins skygazing in the vicinity of a robin delivering a *seet* call on 16 of the 29 days. This behavior was not observed in response to terrestrial predators or the terrestrial alarm calls, *yeeps* and *chucks*.

The behavior of robins hearing white-noise in the playback experiments differed strongly from that of robins hearing *seet* calls. No robins stopped foraging after a playback of white-noise; in contrast, all robins stopped foraging when they heard the *seet* call ($\chi^2 = 20.0$, $P < 0.0001$). Most robins stopped foraging almost immediately upon hearing the call; the average time between hearing the call and stopping foraging was 2.6 ± 0.8 sec, and values for this lag time ranged from 1 to 8 sec. Robins often engaged in one of the three anti-predator behaviors we recorded; 90% scanned the sky, 80% stood alert, and 50% engaged in skygazing. Robins hearing playbacks of *seet* calls engaged in these behaviors for signifi-

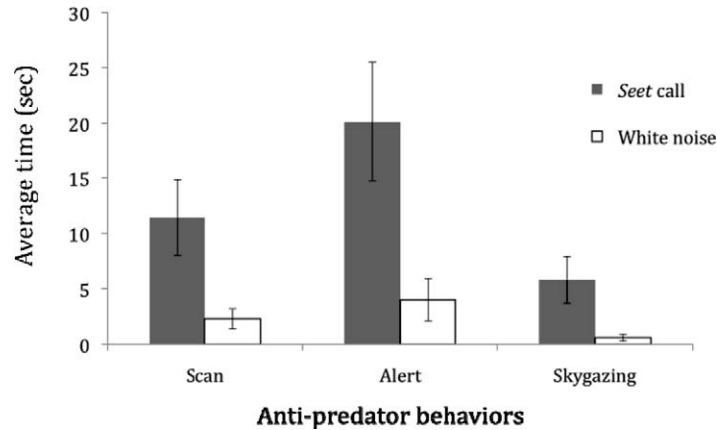


FIG. 3. American Robins spend significantly more time scanning (ANOVA, $F_{1,18} = 6.14$, $P = 0.0234$), alert (ANOVA, $F_{1,18} = 7.12$, $P = 0.0156$), and skygazing (ANOVA, $F_{1,18} = 5.51$, $P = 0.0306$) after hearing a playback of a *seet* call as compared to white-noise.

cantly more time than did individuals hearing white-noise (Wilk's Lambda $F_{3,16} = 8.14$, $P = 0.0016$; Fig. 3).

DISCUSSION

Our investigation supports the early observational accounts reporting the American Robin *seet* call is an aerial alarm. *Seet* calls were only given in response to aerial predators, and robins altered their behavior upon hearing playbacks of the call. They also engaged in a novel anti-predator behavior, skygazing, which presumably allows the robin to scan the sky for danger. A more appropriate test of the function of skygazing would be to compare behaviors after hearing all three call types, *seets*, *yeeeps*, and *chucks*. We did not test this function of skygazing, but preliminary results from playbacks of *chuck* calls (not reported here) and observational data support our findings that skygazing occurs only in response to *seet* calls. Future work should be conducted to understand the exact conditions that elicit this behavioral response, i.e., whether robins skygaze more or less often when the risk of predation is higher.

The bouts we recorded lasted ~ 3 min on average, but we often heard robins giving *seet* calls for longer durations. Several robins in different areas of the park could be heard giving *seet* calls for extended periods of time, >30 min on one occasion. It was difficult to discern if robins in one area called after hearing a robin calling in another area of the park;

however, no robin gave a *seet* call after hearing the *seet* playback. It is easy to see how these calls might have been classified as contact calls, especially considering that an aerial predator is often not visible when robins are calling. An accipiter was only visible to us in our observations on about half of the days we heard robins engaging in *seet* call bouts, most likely because we failed to see the raptor as it flew between patches of trees.

Numerous birds have developed high-pitched alarm calls in response to aerial predators including Wood Thrush (*Hylocichla mustelina*) (Saunders 1961), Tufted Titmouse (*Baeolophus bicolor*) (Morse 1970), Bank Swallow (*Riparia riparia*) (Windsor and Emlen 1974), Black-capped Chickadee (*Poecile atricapillus*) (Ficken and Witkin 1977), and Rufous-backed Robin (*Turdus rufopalliatu*) (Grabowski 1979). High-pitched calls, like robin *seet* calls, are difficult for predators to localize (Marler 1955, 2004; Brown 1982; Jones and Hill 2001). It is likely these calls evolved as warnings for birds other than the predator, unlike the robin's other mobbing calls (Shedd 1982, Gottfried et al. 1985). Two generally recognized explanations for evolution of warning calls are reciprocal altruism and kin selection (Klump and Shalter 1984). The cost of giving a call must be low relative to the benefit gained by receivers for reciprocal altruism to evolve, and signalers must have a high probability of encountering one

another repeatedly (Trivers 1971, Axelrod and Hamilton 1981). *Seet* calls likely have a relatively low cost for the signaler given they can not be easily distinguished by predators. *Seet* calls may therefore fit the criteria for evolution through reciprocal altruism. *Seet* calls may have also evolved through kin selection.

Our study was conducted after the breeding season, during a time when juveniles were independent from their parents. The relatedness of individuals in a foraging flock is unknown for robins (Sallabanks and James 1999); however, it is likely that some flock mates may be related, leading to benefits for kin when an individual gives alarm calls. Another possibility to explain evolution of *seet* calls in robins is that the confusing nature of the calls acts to increase an individual's direct fitness, i.e., emitting *seet* calls directly deters predators by minimizing their ability to locate and capture the individual emitting the call.

Our data do not allow us to discriminate among these mechanisms, but they are testable. If alarms are given when robins are foraging alone, it would suggest the calls have direct fitness benefits. If calls are only emitted in flocks, it is likely they evolved, at least in part, to warn kin or other conspecifics. It would be necessary to track whether robins emit these calls more often in the presence of dependent young than in their absence to discriminate between these two possibilities. Testing these predictions will lead to a better understanding of how these important signals evolved in the American Robin.

ACKNOWLEDGMENTS

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Habitat Selection of Least Flycatchers Includes Deciduous Regeneration in Pine Plantations

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ABSTRACT.—Least Flycatchers (*Empidonax minimus*) are socially monogamous birds that exhibit clustered nesting behavior. We examined the potential influence of forest structure in habitat selection, and formation of Least Flycatcher clusters within a habitat type not previously studied in this species: red pine (*Pinus resinosa*) plantations. We documented 10% less understory vegetation, 13% greater canopy cover, and 30% more deciduous trees in occupied than in adjacent, unoccupied, yet available habitat in 12 clusters in pine plantations. Well developed canopy cover and deciduous foliage appear to provide visual cues for Least Flycatchers when selecting habitat for breeding. Received 3 July 2008. Accepted 10 December 2008.

Studies of clustered nest patterns in birds have focused on both ecological and social factors that might promote this apparent sociality (Ward and Schlossberg 2004, Tarof et al. 2005, Ahlering et al. 2006). Conspecific attraction is a social behavior that may influence settlement patterns whereby individuals are attracted to the presence of other individuals of the same species and subsequently establish adjacent territories (Stamps 1988). Conspecific attraction may be a cue to (perceived) habitat quality (VanHorne 1983); however, preference for a particular habitat may also be cued by vegetation structure (Hildén 1965, Sherry and Holmes 1985).

Clustered nesting in all-purpose territories has been observed in at least five species of

North American songbirds: Yellow Warbler (*Dendroica petechia*; Clark and Robertson 1979), Henslow's Sparrow (*Ammodramus henslowii*; Cully and Michaels 2000), Loggerhead Shrike (*Lanius ludovicianus*; Etterson 2003), Baird's Sparrow (*Ammodramus bairdii*; Ahlering et al. 2006), and Cerulean Warbler (*Dendroica cerulea*; Roth and Islam 2007). Clustered breeding may occur in some species for competitive exclusion, predator defense, use of patchy resources, or from social factors including increased potential for extra-pair copulations (reviewed in Tarof and Ratcliffe 2004). These hypotheses have been examined with mixed results to explain clustered nesting behavior of Least Flycatchers (*Empidonax minimus*) (Sherry and Holmes 1985, Perry and Andersen 2003, Tarof and Ratcliffe 2004, Tarof et al. 2005).

Least Flycatcher clusters occur within a patch of apparently homogeneous forest habitat while other areas within the same patch are left unoccupied (Breckenridge 1956, Perry and Andersen 2003). All previously reported studies involving clustering behavior of Least Flycatchers have been conducted in predominately deciduous forests. Our objective in this study was to identify breeding habitat characteristics of Least Flycatchers in red pine (*Pinus resinosa*) plantations. Studying different habitat types used by Least Flycatchers may further our understanding of habitat selection and links to clustering behavior in this species.

METHODS

Study Area.—We studied Least Flycatchers at Ganaraska Forest (44° 5' N, 78° 30' W) 30

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km south of Peterborough, Ontario, Canada (hereafter, the Forest) from late May to mid-July 2007. The Forest is a 4,280-ha tract comprised of ~50% pine plantation and 50% mixed hardwoods in contiguous patches. Pine plantations are predominately red pine. The mixed hardwood forests are predominately sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), red oak (*Quercus rubra*), and white birch (*Betula papyrifera*). The red pine plantation stands are 25 to 70 years of age and have been managed using row thinning and subsequent selective thinning every 10–15 years (S. McMullen, Ganaraska Region Conservation Authority, pers. comm.), which promotes the growth of deciduous trees. The predominant sapling species are red oak and black cherry (*Prunus serotina*), and ground cover is largely poison ivy (*Toxicodendron radicans*). The terrain is generally undulating to hilly and is underlain by glacial-fluvial deposits, primarily of sand or sandy-loam texture (Tedford 1978).

Mapping Clusters.—Observations were made in areas within the Forest where Least Flycatchers were nesting. We chose 12 red pine plantations in which to map clusters based on presence of two or more calling males within ~75 m of conspecifics. Conservative estimates indicate 12 clusters were occupied by 2–7 territorial males with a mean density of 3.6 males/ha. Delineation of cluster boundaries was conducted between 25 and 30 June from 0600 to 1100 hrs EDT. We walked the perimeter of the cluster from an arbitrary starting point within each chosen area of known Least Flycatcher location. We stopped every 50 m to perform a 2-min point count survey to listen for calling males and to record the location using a Global Positioning System (GPS) (Garmin GPS 12, Garmin International Inc., Olathe, KS, USA.). The Least Flycatcher has a distinctive song, *chebec*, which males sing frequently during the breeding period, up to 60 times/min (MacQueen 1950) making them easy to distinguish and locate. GPS locations were plotted and connected to form polygons.

Habitat Characteristic Measurements.—We compared forest vegetation characteristics in occupied areas (inside clusters, $n = 12$) with adjacent unoccupied, but available areas within the same plantation forest patch (outside

clusters, $n = 12$). A 5×10 m rectangular plot was established centrally within occupied areas. All vegetation plots in unoccupied areas were >50 m from the delineated cluster boundary to preclude any possibility of cluster boundary discrepancy. Vegetation plots between 50 and 100 m from cluster boundaries should represent unused, but available habitat (Jones 2001) because all feeding and nesting occur within their respective territories (i.e., all-purpose territories).

Vegetation characteristics sampled in occupied and unoccupied areas included percent living ground cover, bare soil, stone, leaf litter, and coarse woody debris (CWD). Vertical layers, based on height and diameter at breast height (dbh) (1.2 m) categories, were estimated using percent cover, regeneration (0.5–1.3 m tall and <2.5 cm dbh), saplings (>1.3 m in height and <2.5 cm dbh), understory (>2.5 m tall and ≥ 2.5 but <8 cm dbh), and sub-canopy (10–20 m tall and ≥ 8 cm dbh). Canopy cover was measured using a Model-C densiometer (Lemmon 1956). The tallest tree in each plot was measured with a clinometer (Korning and Thomsen 1994), and basal area was estimated using a factor-2 prism sweep (Arsenault et al. 2006). All trees (≥ 8 cm dbh) and saplings, dead or alive, within each plot were identified to species.

Statistical Analysis.—Tests for normality and homogeneity of variance were performed on the data. Square-root or arcsine were used when data did not meet these assumptions. All tests were performed using an α of 0.05.

We compared habitat characteristics between occupied and unoccupied areas using Student's t -test for all variables except number of trees where the unequal variance t -test was used because, even with transformation, this variable was not normally distributed. Bonferroni corrections were not used to minimize the probability of Type II error (Moran 2003).

Tree (≥ 8 cm dbh) species counts were combined into two groups: coniferous (including red pine, white pine [*Pinus strobus*]), and deciduous (black cherry, red oak, white oak [*Quercus alba*], white birch, American beech, and sugar maple), and compared between occupied and unoccupied areas using a two-tailed Fisher's exact test. Means and \pm SE are presented as untransformed values. All statistical analyses were performed with STATISTICA[®] (Version 7.0; StatSoft Inc. 2004).

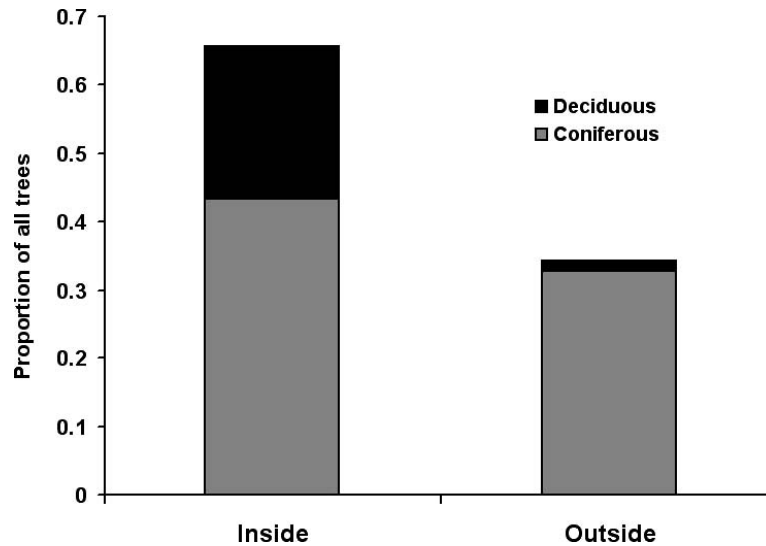


FIG. 1. The proportion of all trees (deciduous and coniferous) inside and outside Least Flycatcher clusters in south-central Ontario red pine plantations, 2007. Sample size = 12 vegetation plots both inside and outside of clusters.

RESULTS

Occupied areas (inside clusters) had more, 15/44 (34%), deciduous trees (≥ 8 cm dbh) than unoccupied areas (outside the clusters) where only 1/23 (4%) were deciduous (Fisher's exact test, $P = 0.007$; Fig. 1). Canopy cover and number of trees ≥ 8 cm dbh were significantly greater inside versus outside the clusters (Table 1). The amount of understory vegetation was marginally significant with greater mean understory cover outside than inside clusters.

DISCUSSION

We report the first use of pine plantations by Least Flycatchers for nesting. Our study suggests that regenerating deciduous trees, as a result of tree thinning operations, attract Least Flycatchers. More deciduous and total number of trees inside Least Flycatcher clusters resulted in greater canopy cover than in red pine plantation sites adjacent and outside these clusters. The greater canopy cover suppressed growth of understory vegetation inside the clusters. Other studies also report

TABLE 1. Habitat variables inside and outside Least Flycatcher clusters in red pine plantations in south-central Ontario, 2007. Statistical significance was ascertained using a t -test for all variables. All sample sizes include 12 clusters and 12 areas outside clusters.

Vegetation variable	Inside clusters	Outside clusters	P
	Mean \pm SE	Mean \pm SE	
Live ground cover, %	36.3 \pm 6.7	44.8 \pm 6.2	0.358
Leaf litter, %	44.0 \pm 6.9	40.8 \pm 6.2	0.732
Coarse wood debris, %	9.3 \pm 1.5	9.4 \pm 2.7	0.967
Regeneration cover, %	6.3 \pm 1.5	20.1 \pm 7.4	0.086
Sapling cover, %	8.2 \pm 1.5	8.5 \pm 3.1	0.912
Understory cover, %	8.2 \pm 3.6	18.8 \pm 3.6	0.052
Sub-canopy cover, %	32.9 \pm 8.6	37.9 \pm 5.9	0.637
Canopy cover, %	84.2 \pm 2.8	71.3 \pm 5.3	0.042
Basal area, m ² /ha	21.3 \pm 1.1	20.3 \pm 1.9	0.853
Tallest tree, m	21.1 \pm 1.0	21.8 \pm 1.0	0.640
Mean number of trees/plot	3.7 \pm 0.7	1.9 \pm 0.2	0.046

Least Flycatcher occupancy was associated with a well-developed canopy (DellaSala and Rabe 1987, Darveau et al. 1992, Perry and Andersen 2003) and a relatively open understory (Breckenridge 1956, Johnston 1971, Sherry and Holmes 1985). Certain structural and compositional features of a forest, such as a minimum required canopy cover, appear to provide visual cues in Least Flycatcher habitat selection.

Clustering was not associated with differences in forest structure in other studies examining the habitat hypothesis (Sherry and Holmes 1985, Tarof and Ratcliffe 2004). This does not imply that habitat selection cues based on structure of vegetation are not used by Least Flycatchers when choosing where to settle. The predominately deciduous forests in these studies may have a homogeneous, well-developed canopy cover which flycatchers may use to form clusters without apparent preference for habitat features within these forests. Relatively dense canopy cover including deciduous foliage may be important for Least Flycatcher foraging. Least Flycatchers use a hovering tactic to glean prey from foliage and may need an open sub-canopy to detect prey movements in the denser main canopy (Robinson and Holmes 1982). Rogers (1985) reported Least Flycatchers use deciduous foliage for foraging more than *Pinus* spp. when compared to the proportion of tree species available.

Habitat selection has fitness consequences and high quality habitats are preferred to increase fitness (Johnson 2007). Cues used as indicators of high quality habitat may include vegetation (Hildén 1965), presence of conspecifics (Stamps 1988, Ward and Schlossberg 2004), or both. Several studies have found that Least Flycatchers respond to song of conspecifics during settlement (Mills et al. 2006, Fletcher 2007), but the first individual to arrive and begin singing in an appropriate habitat must be cued by something other than conspecific attraction (Roth and Islam 2007, but see Betts et al. 2008). Least Flycatchers may be stimulated to settle in habitats, including red pine plantations, with a relatively closed canopy due to presence of deciduous trees. This may be a basic, yet essential, component of Least Flycatcher habitat defining the innate cue used by the first males arriving and

establishing territories. However, a full deciduous canopy may not provide an explanation for clustered breeding.

Several alternate hypotheses for aggregating behavior in Least Flycatchers have been proposed. Clustering during breeding may have (1) a predator deterrence effect through mobbing and alarm calls (Perry and Andersen 2003), (2) a means of competitive exclusion of American Redstarts (*Setophaga ruticilla*) (Sherry and Holmes 1988), or (3) may be in response to female pursuit of extra-pair copulations and formation of hidden leks (Tarof et al. 2005). No study has reported conclusive and consistent results to explain clustering, but most studies have found some evidence related to these hypotheses. Least Flycatchers may benefit in several ways from clustering behavior; each benefit may be acting synergistically to promote and/or maintain the behavior. Our study suggests a necessary precursor to formation of Least Flycatcher clusters is a deciduous habitat component.

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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 (Silllett 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 inter-

val and as 0 if all nest contents were destroyed. We fit a model with covariates for date, date², and date³ 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 $1 - \text{daily survival}$.

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: $F_1 = \sum_{k=3-21} (s^k \times m)$. 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 (Tenant 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 $\geq 90\%$) 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 (Sillert 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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Depredation of Black-throated Blue Warbler Nestlings by an Introduced Slug (Arionidae)

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ABSTRACT.—Black-throated Blue Warblers (*Dendroica caerulescens*) are subject to nest predation by a variety of avian and mammalian species. I present evidence that slugs (Gastropoda: Mollusca) can also function as nest predators. On two occasions, slugs were observed feeding on 6–7 day-old nestling Black-throated Blue Warblers at Hubbard Brook Experimental Forest, New Hampshire, USA. This is apparently the first report documenting that slugs can function as avian nest predators. Received 22 February 2008. Accepted 25 December 2008.

Black-throated Blue Warblers (*Dendroica caerulescens*) are shrub-nesting Nearctic-neotropical migrant passerines. These warblers are subject to nest predation by a wide variety of mammals and birds, including red squirrels (*Tamiasciurus hudsonicus*), eastern chipmunks (*Tamias striatus*), Blue Jays (*Cyanocitta cristata*), and Sharp-shinned Hawks (*Accipiter striatus*) (Holmes et al. 2005). Slugs are rarely but consistently noted in or on Black-throated Blue Warbler nests at a study site in New Hampshire, USA (R. T. Holmes, unpubl. data). However, no evidence exists to indicate that slugs can function as avian nest predators. I present evidence that, at least in rare instances, slugs will feed on nestling Black-throated Blue Warblers.

OBSERVATIONS

Observations were made during summer 2006 at the Hubbard Brook Experimental Forest (43° 56' N, 71° 45' W), a 3,160-ha reserve within the White Mountain National Forest. Black-throated Blue Warblers have been intensively studied at Hubbard Brook and more than 2,900 nests have been monitored since 1986 (Holmes et al. 2005).

On 24 June 2006, during a routine nest check, a field technician found a nest that had

disintegrated, and the three nestlings were on the ground underneath the nest. The nest had apparently been damaged by heavy rains the previous day, and the nestlings had fallen through the nest bottom. The nestlings were 7 days of age and too young for independent movement (Black-throated Blue Warbler nestlings generally fledge 9 days after hatching; Holmes et al. 2005). All nestlings were still alive, although a slug was attached to each bird. One slug was attached to the upper wing of a nestling, while the other two slugs were each attached to the underside of a nestling wing. The nestlings were likely weakened due to their poor ability to thermoregulate. However, they were sufficiently strong to beg actively for food, and showed no evidence of injury other than lesions where the slugs were attached. Both parents were nearby, attempting to feed the nestlings. The field assistant at the site decided to remove the slugs, and replaced the nestlings in the remnants of the nest. None of the nestlings were observed during the subsequent nest check 2 days later, and the adults had begun building a replacement nest. The principal cause of apparent nestling mortality is unclear.

A second observation occurred on 4 August 2006 at a second study area within Hubbard Brook, ~5 km from the site of the first observation. As I approached a nest during a routine nest check, I observed a slug inside the nest actively feeding on a nestling. All four nestlings in the nest had suffered severe disfigurement, and three had died by the time I arrived. The remaining live nestling was weakly attempting to beg for food, despite its injuries. The slug was feeding on a nestling which had already died, and I did not observe a slug feeding on the remaining live nestling. The pattern of disfigurement found on all nestlings was inconsistent with damage previously observed in depredated nests at Hubbard Brook (R. T. Holmes, N. L. Rodenhouse, and

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T. S. Sillett; pers. comm.), suggesting the slug was the sole source of damage to the nestlings. Specifically, all four nestlings had suffered the complete loss of at least one eye, and two nestlings, including the live nestling, had suffered damage to their bills. Eyes were cleanly removed rather than partially pecked or chewed, and no scratches or cuts were evident near the eyes. Damage to the nestlings' bills was extensive with approximately two-thirds of the upper mandible consumed on the live nestling. I observed no scratches or cuts near the bills, which would be consistent with evidence of an avian or mammalian predator. The nest was still being attended by the female, although the male had deserted. Male Black-throated Blue Warblers frequently abandon nests after late July, but females can typically raise late-season young without male assistance when food levels are sufficient, as they were in late July 2006 (Holmes et al. 2005; R. T. Holmes, unpubl. data). Thus, it is unlikely the nestlings had been weakened or died due to starvation prior to being consumed by the slug.

DISCUSSION

The slugs observed in both instances were members of the genus *Arion* (Arionidae), presumably the same species. This genus is native to Europe, but many *Arion* species have successfully established populations in North America (Chichester and Getz 1973). The slugs observed were most likely *A. subfuscus*, which has been previously documented at Hubbard Brook (Strayer et al. 1986; T. A. Pearce, pers. comm.).

A thorough search of the ornithological and malacological literature revealed no prior evidence of slugs feeding on birds, nor on other live vertebrate prey. Most terrestrial slugs, including Arionidae, feed primarily on plant and fungal matter (South 1992). However, *Arion* consume a wide variety of food items, including food of animal origin such as mammal and bird carcasses, dead invertebrates, and con-specifics (Boycott 1934, South 1992).

It is perhaps surprising that slugs have not been previously documented as nest predators given their wide dietary breadth and ability to

consume animal matter. However, the predation events described may represent unusual circumstances. The nestlings in the first incident had fallen from their nest onto the ground. Slugs were much more likely to encounter the nestlings outside of the nest, and the adults may have been less able or willing to dislodge slugs from their young on the ground. In the second instance, the male had abandoned the nest and the task of nest defense was left to the female. Previous observations of this nest indicated the female was extraordinarily wary, and may have been too skittish or inattentive to attack or drive off the slug. It is likely that when slugs encounter nests during the nestling stage, adults will successfully repel slugs, and slugs may only function as nest predators under atypical circumstances.

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Nest Sharing between an American Robin and a Northern Cardinal

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ABSTRACT.—Mixed-clutch nest sharing was observed between an American Robin (*Turdus migratorius*) and a Northern Cardinal (*Cardinalis cardinalis*) in Saylor Township, Polk County, Iowa in May 2007. The nest contained three American Robin eggs and two Northern Cardinal eggs, but only American Robin young were fledged successfully. This was not a case of brood parasitism, as both females were observed alternating incubation of the nest. Competition for desirable nest sites might be a possible cause for this type of interspecific behavior. Received 17 July 2008. Accepted 15 October 2008.

Both intra- and interspecific interactions among birds can have significant influences on nesting success. For example, brood sharing, brood parasitism, nest usurpation, and interspecific feeding have been documented among passerines (Payne 1977). Nest usurpation is often restricted to species with enclosed or cavity nests (Lindell 1996), but other interactions have been observed across a variety of cup-nesting species (e.g., Payne 1977, Shy 1982, McNair 1984). Brood parasitism of Northern Cardinal (*Cardinalis cardinalis*) is known to occur, mainly from Brown-headed Cowbirds (*Molothrus ater*) (Halkin and Linville 1999). Intraspecific brood sharing has also been observed between two female Northern Cardinals, and was attributed to fertilization of both by the same male (Rice 1969). Cardinals have also exhibited intraspecific cooperative breeding behavior among unrelated individuals (Halkin and Linville 1999), as well as an instance of feeding of American Robin (*Turdus migratorius*) young (Shy 1982). American Robins, however, are less tolerant of nest violations, gen-

erally rejecting Brown-headed Cowbird eggs (but see Lowther 1981), and have not been observed to exhibit intraspecific cooperative brood care (Sallabanks and James 1999).

Examples of interspecific nest sharing, where eggs from both species are present in the nest and/or cared for by both species, are less commonly documented, but not absent from the literature (e.g., Cohen 1899, Atkins 1916, Bleitz 1956, Crowell et al. 1982). One example of this phenomenon documented a clutch of 17 larger and nine smaller eggs being jointly incubated by a female Greater Scaup (*Aythya marila*) and a female Lesser Scaup (*A. affinis*) on Great Slave Lake (Fournier and Hines 1996). The eggs were positioned in the nest so both females could sit side by side, in contact with each other, and incubate all of the eggs simultaneously (Fournier and Hines 1996). Mixed clutches have also resulted in mixed broods; during a 10-year field investigation of cavity nesting species, Robinson et al. (2005) observed fledglings of both Red-breasted Nuthatches (*Sitta canadensis*) and Mountain Chickadees (*Poecile gambeli*) after adults of both species had exhibited parental behavior at a single nest. We report a case of interspecific nest sharing and brood care by a pair of Northern Cardinals and a pair of American Robins.

OBSERVATIONS

On 3 May 2007, PWG observed an American Robin in a nest constructed ~1 m above ground level in a 2-m tall Sunkist Arborvitae (*Thuja occidentalis* “Sunkist”). The evergreen was in a suburban development, 2 m from a house and adjacent to a raised wooden deck. The nest was partially sheltered by these structures. The surrounding neighborhood lacked mature trees or much shrub cover. On 4 May 2007, a female Northern Cardinal was observed using the same nest. These two birds changed their respective occupation of the nest frequently and, while each was away

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FIG. 1. American Robin and Northern Cardinal eggs incubated in the same nest.

from the nest, were observed in close proximity to a conspecific male. These males were presumed to be the mates of each female, which was confirmed for the cardinal by subsequent observations.

Examination of the nest on 5 May 2007 revealed three robin eggs and two cardinal eggs (Fig. 1). The nest was monitored *ad hoc* over the next week to document incubation. Regular shifting of females on the nest continued during this period, however, the distance between the females and the nest continually decreased. Quite often, the female cardinal would return to the nest to find the robin on the eggs and perch several centimeters away on a limb. As time progressed, it was common to see both the female cardinal and the female robin in the nest at the same time. This practice appeared to cease when the female cardinal began to display aggressive behaviors toward the robin. If the female cardinal re-

turned to the nest and found the robin there, the cardinal would stand on the back of the robin and scratch and kick until the robin fled the nest. During this time, it was also common to observe the male cardinal bringing food to the female while she sat on the nest.

A fledgling appeared in the nest on 14 May 2007, and both females continued to share nest time, with the male cardinal continuing to feed the female while she roosted on the nest. A second fledgling was present in the nest on 16 May 2007. From this point forward, the cardinals were no longer seen at the nest. Subsequent inspection of the nest revealed only the two fledglings and remains of a single cardinal egg on the ground directly beneath the nest. The two fledglings continued to develop under parental care of the robin, only, and were recognizable as juvenile American Robins on 22 May 2007. The juveniles eventually forayed onto the deck from the nest

and in a matter of days were no longer seen in the area, as was true of the parents.

DISCUSSION

The nesting strategy that uses the active takeover of a nest site of one species by a different species for egg laying and incubation is known as nest usurpation or nest piracy. This particular behavior is not in agreement with the popular belief that coexisting species have divergent nest placement (Lindell 1996). However, studies have also concluded that convergence upon a nest site by more than one species is evidence of interspecific competition for nesting sites (Lindell 1996). The nesting behavior we observed demonstrates a single nest site can be suitable for more than one species. Whether the cardinal pair observed in this instance was two juvenile birds with little nesting experience or was competitively inferior to the robin pair are unresolved questions. The aggressive nature of this particular observation suggests the value of nesting sites in suburban habitats is worth protracted physical confrontation. The Northern Cardinal may use an aggressive re-nesting strategy in response to high levels of nest predation (Filliater et al. 1994), and the selective pressures that affect the evolution of nest site selection require further research for both species.

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Misdirected Parental Care by a Male Eastern Towhee at a Wood Thrush Nest

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ABSTRACT.—Misdirected parental care, or care directed toward unrelated young, has been recorded for many bird species. The Wood Thrush (*Hylocichla mustelina*) is not known to practice this behavior or allow other species to attend to its young. We observed a Wood Thrush nest with three Wood Thrush nestlings and one Brown-headed Cowbird (*Molothrus ater*) nestling being attended by a male Eastern Towhee (*Pipilo erythrophthalmus*). The towhee fed the young of both species in the nest for at least 5 days and was subsequently observed feeding a Wood Thrush fledgling. The towhee also participated in nest maintenance and defense. The proximate cause of towhee attendance at the Wood Thrush nest remains unknown, but begging calls from the nestlings may have stimulated the behavior. Received 28 June 2008. Accepted 3 November 2008.

Misdirected parental care is intra- or interspecific care directed toward the young of an unrelated bird (Shy 1982, Price et al. 1983). Misdirected parental care differs from interspecific feeding, which also may include an adult of one species feeding an adult of another species (Boix-Hinzen 1997). Misdirected parental care has been described several times for the Eastern Towhee (*Pipilo erythrophthalmus*), but Wood Thrushes (*Hylocichla mustelina*) are not known to exhibit this behavior or cooperate as recipients of the behavior in the wild. Skutch (1961) reported an adult male Wood Thrush helped feed nestlings of several different species in an aviary. Shy (1982) reported four occurrences of the Eastern Towhee feeding young of other species, including Field Sparrow (*Spizella pusilla*), Northern Mockingbird (*Mimus polyglottos*), and House Finch (*Carpodacus mexicanus*).

We report the first case of Wood Thrush nestlings in a nest parasitized by the Brown-headed Cowbird (*Molothrus ater*) being fed by a male Eastern Towhee.

Wood Thrush nests were located and monitored during the 2006 field season as part of a long-term study of Wood Thrush breeding ecology in the 15-ha University of Delaware Woods (UDW) in Newark, Delaware (Brown and Roth 2002, 2009). Individually color-banded adults were associated with each nest and assumed to be the social parents of young Wood Thrushes in the nest. An 80-mm spotting scope was used to conduct observations from a blind approximately 15 m from the nest for at least 1 hr/day for each of eight nests in a separate observational study (Schaeffer 2007). It was during these nest observations that KMS discovered a male Eastern Towhee feeding Wood Thrush nestlings and a Brown-headed Cowbird nestling in a Wood Thrush nest (Fig. 1).

OBSERVATIONS

The Wood Thrush nest of interest was discovered on 25 May 2006, ~4.5 m above-ground in a shadbush (*Amelanchier* spp.), and contained three Wood Thrush eggs and two Brown-headed Cowbird eggs. Three thrushes and one cowbird hatched and survived to fledge.

We observed the male Eastern Towhee carrying food near the Wood Thrush nest during the first nest observation period for this nest on 14 June 2006, when the young were 8 days of age. The towhee did not approach the nest while the female was brooding, but remained on a branch 10–15 cm distant. The young thrushes were gaping while being brooded and the cowbird was begging loudly; these behaviors appeared to be directed at the towhee because all young were facing in his direction. Once the female Wood Thrush left the nest, the towhee approached the rim and fed one

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FIG. 1. Female Wood Thrush brooding her begging young as a male Eastern Towhee approaches the nest with food. Photograph by M. E. Zuefle and W. P. Brown, 2006.

young before quickly departing. The Wood Thrush parents did not react to the presence of the towhee. It is likely the towhee had been feeding the nestlings before 14 June based on the insistent begging behavior of the young at the approach of the towhee, the indifferent behavior of the Wood Thrush nest owners, and the rather direct route the towhee took to the nest.

The towhee participated in feeding and several other aspects of nest activity during the six subsequent 1-hr observation periods from 15 June to 20 June. We removed the Wood Thrush nestlings for banding on 15 June, and the towhee called agitatedly while in close proximity to the Wood Thrush parents, which also were scolding. The towhee was observed removing fecal sacs from the nest on 16 June. The towhee continued to take part in nest defense on 17 June, responding to the presence of a Great Horned Owl (*Bubo virginianus*) ~90 m from the nest. The towhee stood on the rim of the nest calling, while two Wood Thrushes, presumably the nest owners, scolded near the owl.

The Wood Thrush parents seldom reacted to the presence of the towhee over the course of our observations. The towhee approached

the nest several times, remaining ~5 cm from the rim, while the female was brooding on 16 June. She did not react to his presence, but the towhee did not try to feed the young. However, when the towhee approached the nest on 17 June while the female was brooding, he attempted to feed one of the nestlings. In response, the female Wood Thrush leaned over the rim and pecked at him. The towhee quickly flew from the nest tree, but remained in the area and returned with food as soon as the female had left the nest. The towhee made eight successful feeding trips while the Wood Thrush parents made seven trips collectively during the 1-hr observation period on 17 June. Both the towhee and female Wood Thrush fed the young on 19 June. The male Wood Thrush did not complete any feeding trips during this 1-hr observation period, but remained in the area singing almost continuously. The Eastern Towhee averaged 3.6 feeding trips/hr compared to the parents' combined 5.2 (2.6/adult) trips/hr for all observations.

The young fledged on the morning of 20 June, and the towhee was observed feeding a Wood Thrush fledgling in the nest tree, ~3 m from the nest and 5 m above ground. The towhee was observed in the same area as the

fledglings until 30 June, after which the fledglings were not observed in the area of the nest. The towhee was not observed feeding fledglings except for 20 June, but heavy cover precluded our efforts to successfully observe the fledglings being fed.

DISCUSSION

We observed misdirected parental care behavior by the male Eastern Towhee over a 7-day period, including the first day the young fledged. Digital photographs of the towhee with food in his bill were taken near the nest on 18 June 2006 (Fig. 1). To our knowledge, this is the first report of Wood Thrushes being the recipient of misdirected parental care in the wild.

Wood Thrushes fledged at 12.3 days of age, on average, during the 2006 field season. The young attended by the towhee fledged at 13 days of age, suggesting the misdirected parental care did not affect nest success.

The circumstances that led the male Eastern Towhee to attend the Wood Thrush nest were unclear, as the breeding status of the towhee was not known. Shy (1982) described eight different categories that might stimulate misdirected parental care. These include the possibility that: (1) the bird practicing misdirected parental care was raising a mixed clutch, (2) the original nest of the bird was destroyed, (3) the nest of another species was close to that of the bird performing the behavior, (4) the calls of nestlings stimulated the misdirected parental care, (5) orphaned birds were adopted temporarily or permanently, (6) a male fed another species while his mate incubated, (7) finding a mateless bird, or being mateless itself, a bird joined a pair with young, or (8) reasons different from those given above.

The Brown-headed Cowbird regularly parasitizes both Wood Thrush and Eastern Towhee nests and the familiar sounds of a begging cowbird, or of nestlings in general, may have been the stimulus that triggered the towhee's feeding efforts. Brown-headed Cowbird parasitism was particularly heavy at UDW during 2006 (12 of 15 nests; Brown and Roth [2004] report annual rates of parasitism at UDW); the same may have been true for

local towhee nests. Yoerg and O'Halloran (1991) and Drózdź et al. (2004) reiterated the potential importance of begging sounds, as well as proximity to nests of other species, as a stimulus for misdirected parental care.

Shy (1982) reported that only 11 of 95 cases (12%) of misdirected parental care involved the feeding of both nestlings and fledglings. Part of this rarity may be due to the difficulty of observing fledglings when they are being fed. The presumed rarity of misdirected parental care also may be due to the lack of systematic nest observations beyond recording the contents of the nest.

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Brood Rearing Ecology of King Eiders on the North Slope of Alaska

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ABSTRACT.—We examined King Eider (*Somateria spectabilis*) brood survival in the Kuparuk oil field in northern Alaska in 2002 and 2003 by monitoring hens with broods using radiotelemetry. We observed complete brood loss in eight of 10 broods. Broods survived less than 2 weeks on average, and most mortality occurred within 10 days of hatch. Distance hens traveled overland did not affect brood survival. Apparent King Eider brood survival in our study area was lower than reported for eider species in other areas. We recommend future studies examine if higher densities of predators in oil fields reduces King Eider duckling survival. Received 26 September 2008. Accepted 18 January 2009.

Declines in the North American population of King Eiders (*Somateria spectabilis*) have increased interest in the status and ecology of this species (Dickson et al. 1997, Gratto-Trevor et al. 1998, Suydam et al. 2000). King Eiders are circumpolar breeders that nest primarily along the margins of freshwater ponds and lakes on the arctic tundra (Suydam 2000). King Eider females leave the nest after hatch with their brood and move over land among tundra ponds (Bergman et al. 1977). Some waterfowl studies hypothesize that distance traveled over land may reduce duckling survival by increasing risk of mortality due to predation or exposure (Rotella and Ratti 1992, Seymore and Jackson 1996), while other studies suggest a positive correlation (Yerkes 2000, Mehl and Alisauskas 2007) or no effect (Wayland and McNicol 1994, Dzus and Clark 1997).

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Estimates of duckling survival for waterfowl species suggest that survival rates are lower from hatching to fledging than during later life stages, and variation in survival is linked to recruitment (Mendenhall and Milne 1985, Johnson et al. 1992). Duckling mortality has been attributed to predation, adverse weather, starvation, and disease (Johnson et al. 1992). Identifying mortality at different life history stages is important for developing conservation plans for King Eiders. We examined survival of King Eider ducklings on the North Slope of Alaska and examined survival in relation to distance traveled over land.

METHODS

Study Area.—We trapped female King Eiders on nests in 2002 and 2003 at the Kuparuk oil field (70° 20' N, 149° 45' W) between the Colville and Kuparuk rivers on the North Slope of Alaska. The site was characterized by numerous thaw lakes, ponds, and basins (Anderson et al. 1999).

Capture and Telemetry.—We searched accessible areas in the Kuparuk oil field for nesting King Eiders during each summer, 2002 and 2003. We candled and floated eggs from nests to assess incubation stage and estimate hatch date (Weller 1956). We monitored nests at least once per week.

We captured hens on nests about 1 week prior to hatch using hand-carried mist nets (Bacon and Evrard 1990) or bow-net traps (Sayler 1962). We originally planned to trap 20 randomly selected hens each year but, due to low nest success we attempted to trap any female still on a nest 1 week prior to predicted hatch date. We captured 12 females in 2002, clipped feathers on their upper back between their wings, and attached 8-g VHF transmitters (Telonics Inc., Mesa, AZ, USA) to the area using epoxy. We attached 10-g VHF anchor transmitters using a suture technique (Pietz et al. 1995) to 12 hens in 2003 to reduce transmitter loss. We checked nests daily after

TABLE 1. King Eider radio-tracking at Kuparuk, Alaska, 2002–2003.

	2002	2003	Total
Females radio-marked	12	12	24
Radio-marked females that failed to hatch eggs	5	3	8
Radio-marked females that lost radio tag	3	0	3
Females radio-tracked	4	6	10
Radio-marked females that lost broods prior to first relocation	0	3	3

capture to document departure of broods. We did not flush hens from nests during these checks. We checked nests for number of hatched eggs when females departed the nest area following hatch. We assumed initial brood size was equal to the number of hatched shell membranes (Girard 1939). All methods and handling of birds were approved by the University of Alaska Institutional Animal Care and Use Committee (IACUC # 02-10).

We located hens after hatch every 2–5 days until ducklings were 30 days of age or until we observed a female without a brood on two consecutive tracking sessions. We tracked marked hens by vehicle, foot, and aircraft. Aerial telemetry flights were used weekly when weather permitted to locate hens not found from the ground. Transmitters had a range of at least 1 km from the ground and up to 10 km from the air. We recorded location information using Global Positioning System (GPS) units and aerial photos. We used aerial photos to record locations when we were not able to get exact GPS locations or did not want to disturb hens with broods. We later returned to these locations to obtain locations using GPS or inferred locations using ArcView. We also recorded brood size, number of hens and ducklings if broods had formed crèches, and predators observed.

Analysis.—We plotted movements of females using ArcView 3.2 Geographic Information System (GIS) (ESRI 1998). We calculated straight line distances between re-observations and mean bearing of movement paths using Animal Movement extension (Hooge and Eichenlaub 1997) in ArcView. We considered survival of a brood as at least one duckling surviving to 30 days of age when King Eider ducklings closely resemble adults in size and mortality from predation is negligible (Mehl and Alisauskas 2007). We considered a marked hen observed in a crèche

to still have a brood if ducklings of the appropriate age tended to follow her rather than alternate hens when disturbed. We calculated daily survival estimates for broods using the Mayfield method and assigned exposure days for complete brood loss equal to 50% of the last observation interval (Mayfield 1961, 1975, Johnson 1979). Survival to 30 days was calculated by raising the daily survival rate to the power of 30.

We used linear regression to test whether the number of days a brood survived was affected by distances traveled over land and if distances traveled per day varied with duckling age. Data from both years were pooled in all analyses due to small sample sizes. We performed all statistical analyses using SAS software (SAS Institute 1990); means \pm SE are presented. Results were considered significant at $\alpha = 0.05$.

RESULTS

Four of 12 hens captured in 2002 were successfully radio-tracked with broods, five failed to hatch eggs, and three prematurely lost their radio transmitters prior to first relocation after hatch (Table 1). Six of 12 hens captured in 2003 were successfully radio-tracked, three failed to hatch eggs, and three lost broods prior to first relocation after hatch (Table 1). We relocated marked hens with broods 5.6 ± 1.4 times ($n = 10$, range = 1–14).

Average brood size at hatch was 4.2 ± 0.4 ducklings ($n = 10$, range = 2–6). We observed complete brood loss in eight of 10 broods (80%). Broods survived an average of 13.4 ± 3.1 days ($n = 10$, range = 2–31). Most brood loss (5 of 8, 62.5%) occurred within the first 10 days after hatch (Table 2). The daily survival estimates for broods was 0.855 ± 0.026 , and estimated survival over 30 days was 10.3% (95% CI: 2.0–49.3). We observed the depredation of a King Eider chick from a

TABLE 2. Number of King Eider ducklings observed in broods of radio-tracked females at Kuparuk, Alaska, 2002–2003. All females experienced complete brood loss within the first 2 weeks after hatch.

ID #	Age (days)			
	Hatch	1–5	5–10	10–15
KIEI02	4	0		
KIEI06	5	3	0	
KIEI17	3	0		
KIEI29	6	3	0	
KIEI68	4	4	1	0
KIEI70	5	5	1	0
KIEI87	3	3	0	
KIEI95	4	3	3	0

tracked brood by a Glaucous Gull (*Larus hyperboreus*) and witnessed two unsuccessful attacks on radio-tracked broods, including one by two Parasitic Jaegers (*Stercorarius parasiticus*) and another by a Glaucous Gull.

Average daily movement rate of hens with broods was 507.4 ± 68.7 m/day ($n = 56$; range = 0–2,376 m). Longer daily movement rates did not affect the number of days a brood survived ($F_{1,8} = 0.10$, $P = 0.76$). Distance traveled per day by hens with broods did not vary with duckling age ($F_{1,54} = 0.90$, $P = 0.35$). Hens did not appear to travel in a particular general direction with ducklings after hatch. Four hens moved east, three north, two south, and one west.

Crèche formation was not extensive; we rarely observed crèches of King Eiders on the study area and only observed two marked hens with broods in crèches. The hens that joined crèches were the only females in our study to successfully raise young to 30 days of age. One marked hen hatched five ducklings, but was later observed with three King and three Spectacled (*S. fischeri*) Eider chicks. We first observed her in a crèche when her chicks were 9 days of age. We later observed this hen in a crèche of up to 40 hens and 12 young. We believe some of these ducklings were still associated with the marked hen based on their behavior. We observed the second successful hen in a small crèche with one other hen when her chicks were 18 days of age; each had a brood of two ducklings. The two broods were discernable by their different ages with the marked hen having smaller, younger ducklings.

DISCUSSION

We offer the first description of survival of King Eider broods in Alaska. We observed lower apparent survival of broods (20%) than observed for King Eiders breeding at Karrak Lake in Nunavut, Canada (35%, Mehl and Alisauskas 2007). Apparent survival of King Eider broods at Kuparuk was also lower than reported for related eider species in Alaska. Half (49%) of all Spectacled Eider (Flint and Grand 1997) and 73% of all Common Eider (*S. mollissima*) females (Flint et al. 1998) on the Yukon-Kuskokwim Delta lost their broods within 30 days of hatch.

Our calculation of apparent survival of broods does not include an estimate of variation in the data. Given our small sample size and probable variation among years, we would assume this variation to be significant. Mayfield estimates of survival for King Eider broods at Kuparuk, while low, show large confidence intervals that overlap with survival estimates for broods at Karrak Lake (31%, 95% CI: 13–50%; Mehl and Alisauskas 2007).

Gull predation has been identified as a primary cause of eider duckling mortality (Mendenhall and Milne 1985, Mehl and Alisauskas 2007). Glaucous Gulls nest across Alaska's Arctic Coastal Plain; studies have indicated their populations may be more concentrated near coastal villages and areas of industrial development such as Kuparuk and Prudhoe Bay (Noel et al. 2006). Other potential predators of ducklings at Kuparuk included Parasitic Jaeger, Common Raven (*Corvus corax*), and arctic fox (*Alopex lagopus*). The population of predators in Alaskan oil fields has increased since development, most likely due to greater access to food from anthropogenic sources such as landfills and garbage dumpsters, and shelter for nesting and denning sites (National Research Council 2003).

We did not observe extensive crèche formation at Kuparuk similar to Mehl and Alisauskas (2007) at Karrak Lake; however, the only hens in our study that successfully raised ducklings joined other females with broods. Crèche formation may increase duckling survival by females jointly caring for young and by larger brood sizes diluting the risk of predation (Eadie et al. 1988).

King Eider brood survival did not improve

with greater distance travelled over land in the Kuparak area in contrast to the findings of Mehl and Alisauskas (2007) at Karrak Lake. We hypothesize the contrasting results of these two studies may be partially explained by habitat composition of the study areas. The Karrak Lake site is a large lake with many islands, while Kuparuk is characterized by small ponds and wetland complexes. Mehl and Alisauskas (2007) hypothesized that movement of broods to smaller ponds from the main nesting areas at Karrak Lake improved survival by providing better foraging, lower gull densities, and more shelter from winds. Movements from nesting locations at Kuparuk would not yield the same benefits because nesting already occurs on small ponds.

We had little evidence to suggest broods not re-observed with hens were adopted, because crèche formation was limited in the study area and we did not observe hens with an unusually large number of ducklings. Our analysis of brood survival underestimated mortality by censoring broods from the analysis that were not re-observed after hatch, but our observations of King Eider broods at Kuparuk suggest that survival of broods may be low. Our findings should be useful for developing a comprehensive investigation of King Eider survival as more King Eider nesting habitat across northern Alaska is leased for resource development. We encourage additional study of King Eider survival on the North Slope of Alaska especially near areas of resource development where survival of ducklings may be depressed by artificially inflated predator populations.

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Diet Composition of Wintering Wilson's Snipe

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ABSTRACT.—We examined diet composition of Wilson's Snipe (*Gallinago delicata*) ($n = 372$) collected along the central Gulf Coast of Texas based solely on upper digestive tract contents. Food items included 11 invertebrate orders, one invertebrate class, and eight plant genera. Oligochaetes were the predominant food throughout the non-breeding period, but snipe consumed fewer ($P = 0.021$) earthworms in spring than in fall. Aquatic insects were frequently

consumed by snipe and during spring represented approximately the same proportion of the diet as earthworms. Plant foods consisted almost entirely of seeds and comprised 9.7–26.8% of the diet throughout the non-breeding period. Wilson's Snipe consumed dipteran larvae more often during spring than fall ($P = 0.056$). Female snipe consumed crustaceans during spring (14.8%), while only trace amounts were found in the diet of male snipe. Differences in the diet of Wilson's Snipe between males and females were probably related to differences in habitat use as well as availability of invertebrates throughout the non-breeding period. *Received 5 March 2008. Accepted 7 September 2008.*

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Studies of Wilson's Snipe (*Gallinago delicata*) suggest that animal foods are a signifi-

cant portion of their winter diet (Erickson 1941, Whitehead 1965, White and Harris 1966, Owens 1967, Booth 1968, Jirovec 1971, Tuck 1972). Most studies suggest aquatic insects and mollusks are the primary animal foods consumed by snipe and discount the importance of earthworms (Oligochaeta). Owens (1967) found earthworms in 50% of the birds he collected in wet cattle pastures in Louisiana, but they accounted for only 21.6% of the total animal volume in the diet. Previous studies stimulated debate over the importance of plant foods in the diet of wintering Wilson's Snipe. Whitehead (1965), Owens (1967), and Booth (1968) found the dry mass of plant materials comprised ~41, 50, and 62% of the diet of wintering snipe, respectively. In contrast, White and Harris (1966) and Jirovec (1971) reported that plant foods accounted for $\leq 20\%$ of the dry mass in the diet.

Inconsistencies between these studies and the conclusion that earthworms are relatively unimportant in the diet of wintering snipe probably occurred because they included gizzard contents in diet composition analysis. This approach biases diet composition toward hard food items (i.e., plant foods or hard animal parts) because the grinding action of the gizzard quickly renders soft foods (e.g., earthworms) unrecognizable (Rundle 1982). This bias can be avoided by examining only the contents of the esophagus and proventriculus (Swanson and Bartonek 1970, Reinecke and Owen 1980, Rundle 1982).

Snipe have long bills with a prehensile tip used to probe moist soils in search of invertebrates (Arnold 1994). Winter habitats used by Wilson's Snipe typically have wet ground (i.e., wet pastures, plowed and fallow rice fields, and coastal marshes) (Arnold 1994), and soil moisture is a primary variable regulating earthworm abundance and distribution (Curry 1998). Our objective was to quantify the diet of wintering Wilson's Snipe based solely on examination of upper digestive tract contents.

METHODS

We conducted this study in the rice prairies and coastal marshes along the central Gulf Coast of Texas from October 1997 through April 1998. Collection sites included five different habitat types: harvested rice fields, fal-

low rice fields, mud flats (i.e., recently disked fallow rice fields), drained impoundments, and coastal marshes. Vegetation communities and land use practices associated with the study area were described by McCloskey (1999).

We collected Wilson's Snipe ($n = 372$) by shooting, systematically alternating between habitat types throughout the non-breeding period. We typically collected four birds per day allocated throughout the day. We examined diet composition by analyzing the contents of the upper digestive tract (UDT) (i.e., esophagus and proventriculus). Each specimen was injected with 2–3 ml of 80% ethanol into their UDT immediately after collection to prevent post-mortem digestion of food items. The UDT contents were subsequently placed into individually labeled nalgene bottles containing 80% ethanol (Swanson and Bartonek 1970). Food items were sorted, classified, and dried to constant mass at 80° C to quantify percent occurrence and aggregate percent dry mass of foods consumed during each season. We separated the non-breeding period into three seasons based on molt intensity of collected individuals. A fall molting period was delineated as 6 October–13 November 1997, a non-molting winter period was delineated as 14 November 1997–4 February 1998, and a spring molting period was 5 February–10 April 1998.

We used Kruskal-Wallis one-way ANOVA (PROC NPAR1WAY; SAS Institute Inc. 1999) to investigate seasonal variation in diet of males and females. We used Dunn's Multiple Comparisons Test (SAS Institute Inc. 1999) to examine any seasonal differences. We used Mann-Whitney *U*-tests to compare diets between males and females within each season.

RESULTS

Sixteen of 39 females and 16 of 30 males contained food in their upper digestive tract during fall. Only 19 of 95 females and 11 of 64 males contained food in their UDT in winter. The proportion of birds with ingesta increased in spring with 26 of 86 females and 17 of 58 males containing food in their UDT. Proportions of male and female snipe containing food were highest throughout spring migration (16 Mar–10 Apr), with 21 of 41 females and 11 of 17 males containing food in

their UDT. Diets of Wilson's Snipe included foods from 11 invertebrate families, one invertebrate class, one vertebrate species, and eight plant genera (Table 1). Snipe fed primarily on animal foods, which represented >73% of the dry mass of the diet throughout the non-breeding period (Table 1). Ninety-one percent of all snipe that contained food in their UDT consumed animal foods.

Oligochaetes (earthworms) were the primary food item of Wilson's Snipe, representing from 33.1 to 67.3% of the dry mass of the diet over the entire non-breeding period (Table 1). There were seasonal differences in Oligochaete consumption ($H = 6.08$, $df = 2$, $P = 0.048$). The diet of male and female snipe contained similar proportions of Oligochaetes during fall and spring but, during winter, earthworms comprised 63.4% of the total food mass of males, compared to only 38.3% for females (Table 1). Oligochaetes comprised a greater proportion of the diet of both males and females during fall than during spring ($P = 0.021$).

Aquatic insects represented 12.4–35% of the diet of male and female Wilson's Snipe. Coleoptera (i.e., Hydrophilidae larvae and unidentified adult parts), Diptera larvae (i.e., Ceratopogonidae, Chironomidae, Culicidae, and Tipulidae), and Hemiptera were the most frequently eaten aquatic insects by male and female snipe (Table 1). There were seasonal differences in the amount of aquatic insects consumed ($H = 10.96$, $df = 2$, $P = 0.004$), with both males and females increasing their consumption during spring. The combined dry mass of Coleoptera, Diptera, and Ephemeroptera in spring represented 33% of the diet for females and 35% for males, which approximated the dry mass of Oligochaetes in the diet during this period (Table 1). Male and female snipe consumed dipteran larvae most often during spring ($P = 0.056$).

Crustaceans were ingested almost exclusively by female snipe with males consuming only trace amounts (i.e., <1%) of isopods during winter and spring (Table 1). Females consumed amphipods and isopods only during winter and spring (Table 1). We found no crustaceans in the UDT of any individuals during fall, and females ate decapods only during spring (Table 1).

The remaining animal foods consisted of Arachnoidea (i.e., Hydracarina), mollusks

(i.e., Gastropoda and Pelecypoda), one southern cricket frog (*Acris gryllus gryllus*), and unidentified invertebrate parts (Table 1). Only females consumed Hydracarina with the majority being consumed during fall and winter. Females consumed mollusks during all seasons, while males consumed gastropods and pelecypods mostly during spring (Table 1).

Plant foods represented $\leq 26.8\%$ of the diet and were detected in $\leq 62.5\%$ of male and female Wilson's Snipe throughout the non-breeding period (Table 1). Seeds, particularly those of *Cyperus* spp., *Eleocharis* spp., and *Polygonum* spp. were the most frequently consumed plant foods (Table 1). *Polygonum* spp. was consumed almost exclusively by females and mostly during fall and winter ($H = 7.534$, $df = 2$, $P = 0.023$). Male snipe consumed only trace amounts of *Polygonum* and only during fall (Table 1). Plant parts (i.e., stems and leaves) were not considered food items because they usually comprised only a trace of the total plant dry mass (Table 1), and were typically found in association with other food items suggesting they were picked up incidentally.

DISCUSSION

The proportion of Wilson's Snipe containing ingesta in their UDT was greatest during fall and spring. These periods coincide with molting, and protein demand may be greater for snipe during these periods (Ankney 1979, Murphy and King 1982). Spring migration occurred between 16 March and 10 April (McCloskey 1999), and aggregate percent dry mass of animal foods was greatest during this time suggesting snipe were storing lipid reserves for migration. Much of the southern portion of the snipe's winter range in the United States is characterized by wet, but relatively warm weather, which results in continuous periods of invertebrate reproduction and growth (Merritt and Cummins 1996). If food is readily available and energy requirements for thermoregulation are relatively low in winter, snipe may alter their foraging strategy to specific times of the day or night. This may partially explain the lower proportion of our sample that contained ingesta in their UDT during winter.

Female snipe consumed a wider variety of invertebrates than males during winter with crustaceans, mollusks, and arachnids compris-

TABLE 1. Aggregate percent dry-mass and percent occurrence of foods consumed by male and female Wilson's Snipe during fall, winter, and spring along the central Gulf Coast of Texas.

Food item	Aggregate % dry mass						Percent occurrence					
	Female			Male			Female			Male		
	F ^a (16) ^b	W (19)	S (26)	F (16)	W (11)	S (17)	F (16)	W (19)	S (26)	F (16)	W (11)	S (17)
Annelida												
Oligochaeta	55.7	38.3	33.1	67.3	63.4	39	62.5	42.1	38.5	75	63.6	47.1
Insecta												
Coleoptera	12.9	2.8	13.1	13	1	21.1	37.5	15.8	26.9	25	9.1	23.5
Diptera	0	6.9	18.4	0	0.2	12.3	0	10.5	30.8	0	9.1	17.6
Hemiptera	0	5.3	0	1.3	9.1	0	0	5.3	0	12.5	9.1	0
Odonata	0	0	0	0	2.1	0	0	0	0	0	9.1	0
Ephemeroptera	0	0	1.1	0	0	1.6	0	0	3.8	0	0	5.9
Mollusca												
Gastropoda	6.3	0.6	6.4	0	0	5.9	6.25	5.3	11.5	0	0	5.9
Pelecypoda	0.1	5.3	3.3	0.02	0	5.9	6.25	5.3	3.8	6.25	0	5.9
Crustacea												
Isopoda	0	3.2	2.9	0	0.4	0.4	0	5.3	19.2	0	9.1	5.9
Decapoda	0	0	8.1	0	0	0	0	0	11.5	0	0	0
Amphipoda	0	6.4	3.8	0	0	0	0	10.5	3.8	0	0	0
Arachnoidea												
Hydracarina	6.2	2.1	0.01	0	0	0	6.25	5.3	3.8	0	0	0
Unidentified												
Invertebrate	0.2	2.3	0.1	0	7.8	0	6.25	15.8	3.8	0	9.1	0
Vertebrate	0	0	0	3.2	0	0	0	0	0	6.25	0	0
Total animal	81.4	73.2	90.3	84.8	84	86.2	93.8	89.5	96.2	87.5	90.9	88.2
Seeds												
<i>Cyperus</i>	3.8	13.9	4.7	7.4	4.4	10	37.5	31.6	11.5	37.5	27.3	23.5
<i>Juncus</i>	0.2	0.2	1.9	2.9	0.04	2.8	12.5	10.5	7.7	31.25	9.1	11.8
<i>Eleocharis</i>	1.2	5.7	0.2	3.8	6.1	0.05	12.5	10.5	7.7	12.5	9.1	5.9
<i>Polygonum</i>	5.6	5.1	1.6	0.7	0	0	25	5.3	3.8	12.5	0	0
<i>Achillia</i>	0	1.7	0	0	0	0.3	0	5.3	0	0	0	5.9
<i>Sisymbrium</i>	0	0	0.5	0	0	0.02	0	0	3.8	0	0	5.9
<i>Echinochloa</i>	1	0	0	0	4.3	0	6.25	0	0	0	0	0
Unidentified seeds	6.5	0	0	0.3	0	0	18.75	0	0	12.5	0	0
Plant parts	0.3	0.2	0.8	0.1	1.2	0.6	25	10.5	19.2	18.75	27.3	17.6
Total plant	18.6	26.8	9.7	15.2	16	13.8	56.25	47.4	42.3	62.5	54.5	41.2

^a Seasonal categories: F = fall period, W = winter period, S = spring period.

^b Sample size.

ing 9.6, 5.9, and 2.1% of their diet, respectively. These food items were essentially absent from the diet of males during winter. These apparent differences in invertebrate use between male and female Wilson's Snipe during winter may be related to differential partitioning of winter habitats (McCloskey and Thompson 2000).

Fall rains flood marshes and probably benefit earthworms initially, which may explain why earthworms were more common in the diet of snipe during fall. However, continued flooding and subsequent drying of soils can increase salinity levels, which can limit earthworm populations (Curry 1998). While earthworms were the predominant food of snipe during fall and winter, aquatic insects became equally important in their diet during spring. Emergence of aquatic insects is synchronized primarily by water availability, temperature, and oxygen levels (Merritt and Cummins 1996), and may explain their increased ingestion during spring. Increased availability of aquatic insects may allow snipe to obtain nutrient stores required for spring migration without expending as much energy.

Previous studies on the diet of wintering Wilson's Snipe reported high frequency of occurrence of seeds, but most discounted their importance suggesting seeds were ingested incidentally while probing for invertebrates (Erickson 1941, Whitehead 1965, White and Harris 1966, Owens 1967, Booth 1968, Jirovec 1971, Tuck 1972). Fritzell et al. (1979) also discounted the importance of seeds, suggesting they were ingested incidentally, remained relatively unchanged during digestion, or would eventually be regurgitated. However, we found UDT contents of nine snipe to be comprised solely of seeds. Booth (1968) found over 45,000 seeds of 48 plant species in gizzards of 260 wintering snipe collected in Louisiana. Although animal foods clearly dominate the diet of wintering snipe, seeds may be an important source of carbohydrates and may be more than just incidentally consumed.

Wintering Wilson's Snipe consume a variety of plant and animal foods during the non-breeding period. Snipe spend ~8 months of the year in wintering areas and the diversity of food types in these areas provide them with energy required for basal metabolic requirements, daily activity, molt, thermoregulation

during cold spells, and migration in spring. Snipe use a variety of habitats on wintering areas that are both permanent and ephemeral in nature (Arnold 1994), which can affect the distribution and abundance of invertebrates throughout the non-breeding period. Thus, snipe need a diversity of habitat types in wintering areas. These habitats should contain moist soils and provide a diversity of plant and animal foods. The ability to identify and maintain potential snipe habitat will become increasingly important with continuing wetland loss along the Gulf Coast of Texas (Moulton et al. 1997).

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An Overlooked Cost for the Velvety Plumage of Owls: Entanglement in Adhesive Vegetation

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and Juan J. Negro¹

ABSTRACT.—We used data collected during 1995–2007 at the only Wildlife Rehabilitation Center on Tenerife Island (Canary Islands) to quantify entanglement mortality of owls. At least 66 of 1,206 Long-eared (*Asio otus*) and 5 of 231 Barn (*Tyto alba*) owls admitted to the Wildlife Rehabilitation Center were entangled in burr bristlegrass (*Setaria adhaerens*). Twelve (18.2%) of the 66 Long-eared Owls died as a result of entanglement while one of five Barn Owls

died. A higher incidence of entanglement occurred during summer, coinciding with seed-head ripening and dispersing recently-fledged owls. Velvety plumage may be an important cost for owls, and responsible for owls acting as seed dispersers. *Received 28 June 2008. Accepted 14 December 2008.*

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Owls have evolved adaptations to hunt in poor light conditions, including frontally located and disproportionately large eyes or, in some species, an asymmetrical placement of the ear openings for improved hearing (del Hoyo et al. 1999). Owls also have feathers with traits which have been considered as adaptations for silent flight. The main structural feather adaptations of owls are: (1) elongated barbs on the leading edge at the outer prima-

ries, (2) a trailing edge on the flight feathers, and (3) modified distal barbules on the dorsal surface of feathers (del Hoyo et al. 1999). The last trait makes velvety plumage easily perceived by the unaided human eye (Mikkola 1983). This plumage is also exhibited by other nocturnal or crepuscular birds, including nightjars (Order Caprimulgiformes), Bat Hawk (*Macheiramphus alcinus*) (J. J. Negro, pers. obs.), and *Elanus* kites (Negro et al. 2006). Silent flight permits owls to go undetected by their prey, and improves their ability to detect noises (Taylor 1994, del Hoyo et al. 1999).

Development of velvety plumage may have associated costs, including increased risk of entanglement in dense vegetation during hunting (Gladyre 1959, Mendelsohn 1983, Nozerand 1994, Molnar 1996). We describe mortality, caused by a grass species, of the resident owl community in the Canary Islands. Only two species of owls regularly breed in the Canary Islands: Long-eared Owl (*Asio otus*) and Barn Owl (*Tyto alba*).

Burr bristlegrass (*Setaria adhaerens*, Family Poaceae) is an annual species, possibly native in the Canary Islands (Izquierdo et al. 2004). It grows in orchards, abandoned farmlands, road ditches, and field margins. It flowers and dries during spring and early summer, and retains ripe seed-heads in the dry plant (R. Mesa, pers. comm.). Ripe seed-heads are adhesive and adapted to exozooecore dispersal.

OBSERVATIONS

Owls admitted during 1995–2007 were identified by the staff of the Wildlife Rehabilitation Center “*La Tahonilla*” (WRC), which annotated recovery circumstances. The center is in Tenerife, the largest island (2,034 km² and 3,718 m of altitude) of the Canarian archipelago (27° 37′–29° 24′ N, 13° 20′–18° 8′ W), and our data correspond to owls found only on this island.

At least 66 (5.5%) of 1,206 Long-eared and 5 (2.2%) of 231 Barn owls admitted were entangled in *S. adhaerens* plants. Entanglement in burr bristlegrass likely occurred when owls were hunting. Twelve of 66 Long-eared Owls (18.2%) and one of five Barn Owls died as a result of becoming entangled in the plants. Most entangled birds that were recovered alive would have died if not found because

owls do not appear capable of freeing themselves from the plant. The highest incidence of entanglements occurred during summer with the largest number of reports in July and August.

DISCUSSION

The interaction between owls and a plant adapted to exozooecore dispersal can be a considerable cause of mortality in the Canary Islands. This factor has been overlooked, despite several published records, and has not been quantified in the literature. Entanglement of owls in vegetation appears to be the result of anthropogenic perturbations in the Canary Islands, even though *S. adhaerens* is possibly a native plant (Izquierdo et al. 2004). Burr bristlegrass is mainly associated with human-affected landscapes and is almost absent in natural areas. The highest densities of *S. adhaerens* are in human-transformed areas, which is where owls tend to become entangled. The temporal pattern with maximum values during the summer, may be related to ripening of seed-heads, as well as to dispersal of fledgling owls (age of affected owls is not available).

Entanglement of birds with velvety plumages has been reported involving Long-eared Owls, Barn Owls, and Black-winged Kites (*Elanus caeruleus*) (Gladyre 1959, Mendelsohn 1983, Nozerand 1994, Molnar 1996). Entanglement as a cause of mortality is not exclusive to birds with velvety plumages. At least two instances involving Common Kestrels (*Falco tinnunculus*) entangled in *S. adhaerens* in the Canary Islands are known (WRC, unpubl. data; J. Curbelo, pers. comm.). The Common Kestrel is the most abundant raptor in the Canary Islands, and >1,200 have been admitted to the WRC in the study period. Whether Common Kestrels become entangled less often than owls due to different plumage characteristics or due to different micro-habitat use remains unknown.

It is possible that some owls escape unscathed from contact with *S. adhaerens*, but seeds of this species may become affixed to their plumage and transported elsewhere. This interaction implies a new ecological role for owls as exozooecore seed dispersers.

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Aggressive Response of Adult Bobolinks to Neck Ligatures on Nestlings

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ABSTRACT.—We monitored provisioning behavior at 18 Bobolink (*Dolichonyx oryzivorus*) nests during 240.5 min of videotape data from June to July 2006, and observed 64 nest visits by adults while nestlings were fitted with neck ligatures. Adults pecked or pulled at the ligatures, often aggressively, at 72% of nests ($n = 18$) and 52% of visits ($n = 64$). These behavioral responses by adults indicate the neck ligature technique is more invasive than previously believed. We documented no mortality as a result of ligature placement, but researchers should minimize the time that ligatures are in place to reduce stress to both parents and nestlings. *Received 8 September 2008. Accepted 30 January 2009.*

Quantitative assessments of avian diets may be critical for evaluating habitat quality. However, methods used to quantify avian diets have associated biases and/or shortcomings as most studies require techniques tailored to specific studies and hypotheses (Rosenberg and Cooper 1990). Neck ligatures have been used to quantify diets of nestling birds as this technique allows collection of prey items prior to onset of digestion. Modifications have been suggested to improve ligature function and minimize negative effects on nestlings. For example, Johnson et al. (1980) described abnormal behavior of nestlings after leaving ligatures in place for 1 hr and suggested that collection of prey immediately after each parental visit would minimize biases. Further, Mellott and Woods (1993) found that cable ties simplified ligature placement compared to coated wire, especially when used by untrained personnel.

Neck ligatures are considered an invasive technique (Rosenberg and Cooper 1990, Poulsen and Aebischer 1995), but most studies addressing their effects have focused on the be-

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havioral responses of nestlings. We used video cameras and neck ligatures simultaneously in a study of nestling Bobolink (*Dolichonyx oryzivorus*) diets. We report on the response of adult Bobolinks to placement of neck ligatures on nestlings.

METHODS

Study Site.—Our study was conducted during June–July 2006 in three hayfields in Hinesburg, Shelburne, and Charlotte, Chittenden County, Vermont, USA. Bobolinks breed in hayfields and pastures throughout this agricultural region (Shustack 2004, Perlut et al. 2006) and their ground nests are relatively easy to locate.

Video and Ligature Data Collection.—Nest observations, video monitoring, and ligature sampling occurred between 0400 and 1300 hrs EST during precipitation-free periods. A small, wide-angle “lipstick” lens (www.helmetcamera.com) was mounted 10 cm from the nest when nestlings reached 6 days of age. The lens was attached by cable to an 8-mm camcorder (Sony DCR-TRV460 Digital8 Handycam) placed 2 m from the nest and concealed by vegetation. Recording sessions commenced with an initial 45-min acclimation period during which nestlings were left undisturbed. Recording was paused while neck ligatures were placed on nestlings following Johnson et al. (1980) and subsequent modifications (Mellott and Woods 1993). We placed ligatures on a maximum of three nestlings per nest using plastic cable ties (10 cm length before cutting off excess, 2.5 mm width), temporarily removing any additional nestlings for the remainder of the videotaping period (generally 45 min). Removal of some of the nestlings reduced the number of nestlings that were not fed by parents during a feeding session (adults were not observed feeding all nestlings in a single feeding trip when a nest contained five or six nestlings; N. G. Perlut, unpubl. data) and reduced the number of nestlings that would be exposed to any potential stress during the ligature process. We attempted to remove ligatures and collect diet samples from the nestlings as soon as we observed the adults return to the nest with food. Prolonged use of ligatures can induce abnormal swallowing and gaping behavior in nestlings, which leads to the redistribution of prey

items among nestlings by adults (Johnson et al. 1980).

RESULTS

We monitored 18 Bobolink nests during 240.5 min of videotape data. We applied neck ligatures to 50 nestlings, and successfully collected 99 prey items from 28 of those nestlings. No nestling mortality occurred while nests were videotaped. Leaf hoppers (27.3% based on numerical abundance), holometabolous larvae (24.2%), grasshoppers (16.2%), mayflies (8.1%), spiders (7.1%), and moths (5.1%) were the most common prey types fed to nestlings. Mean \pm SD prey length was 14.5 ± 10.2 mm with 17% of prey items delivered >25 mm. Sixteen of the 18 nests were successful with 56 nestlings fledged.

We observed 64 nest visits by adults while nestlings were fitted with ligatures. Seventy-two percent of visits were by females and 28% by males. On average, females and males visited nests 2.6 and 1.0 times, respectively while ligatures were in place (~ 45 min). Adults pecked at ligatures of nestlings in 13 of 18 nests (72%) and in 33 of 64 (52%) visits. They directed pecks at more than one nestling in 70% of the visits during which adults pecked at the ligatures. Females had a greater propensity to peck at ligatures with 59% of all female visits eliciting pecks to ligatures compared to 33% of all male visits. The first adult to return to the nest pecked at the ligatures in 12 of 13 nests in which adults pecked at ligatures. There was no indication that probability of pecking changed across the time period ligatures were in place (logistic regression, $\chi^2 = 1.68$, $df = 1$, $P = 0.20$).

Adults generally pecked at the thin band of the cable tie. In these cases, the adults appeared to be assessing whether or not the ligature could be easily removed from the chicks. Adults also grasped and pulled at the bulkier locking mechanism of the cable tie with the appearance that removal was the goal. Parents were notably aggressive in about half of the nests in their attempts to remove the ligatures, grasping the ligature and forcibly pulling the nestlings' heads upwards or sideways. In one instance, a female inspected, grasped, and pulled at a nestling's ligature for 30 sec. No aggressive actions toward nestlings were noted when ligatures were not present

on nestlings based on video data prior to ligature placement and a few tapes which we left running after the ligature sessions. One female visually inspected her nestling's throats upon her first visit to the nest ~20 min after removal of the ligatures.

DISCUSSION

Use of neck ligatures has been shown to provide quality dietary data for nestling birds (Orians 1966, Martin et al. 2000, Clotfelter et al. 2007). Our data support these results as we were able to collect a relatively large sample of prey items over a short period of time. Prey length data suggest that adults did not adjust the size of prey items brought to nestlings with ligatures. However, we do not have adequate control data (nestlings without ligatures) for a quantitative comparison.

Our data show that undesirable behavioral responses to ligatures are not restricted to nestlings. The strong and consistent response of adults to ligatures suggests this technique elicits stress that was not previously documented. Attempts by female Red-winged Blackbirds (*Agelaius phoeniceus*) to remove pipe cleaner ligatures have been documented, but no behavioral data were provided (Robertson 1966). Our results indicate that Bobolinks are strongly attuned to the appearance of their nestlings and, in most cases, neck ligatures trigger a response upon the first visit to the nest. Females in our sample were more likely to attempt to remove ligatures than males (but also made more nest visits). Approximately half of the attempts to remove the ligatures were aggressive with parents lifting and/or dragging nestlings by the ligature. These responses indicate the neck ligature technique is more invasive than previously believed. Comparable data from other species would be useful to better address the generality of our findings.

Gaunt and Oring (1999) noted the potential for changes in blood circulation, tracheal function, and food delivery rates with use of neck ligatures. Our data suggest there may be additional stress to nestlings beyond physical placement of the ligatures. The majority of nest visits by adults included pecking or pulling at neck ligatures and there was no indication that adults became habituated to the presence of ligatures. Neck ligatures remain a

relatively safe, inexpensive, and informative method, but do present welfare concerns. Investigation into the efficacy of less-invasive alternatives such as videography should be conducted, especially when working with rare and declining species. We documented no mortality as a result of ligature placement, but researchers should minimize the time that ligatures are in place to reduce stress to both parents and nestlings.

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