

BROAD-WINGED HAWK NESTING BEHAVIOR IN FORESTED LANDSCAPES OF PENNSYLVANIA

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ABSTRACT.—Broad-winged Hawks (*Buteo platypterus*) concentrate in large numbers during migration but several sources suggest regional declines in eastern North America may be occurring, perhaps due to increasing human development, natural resource exploitation, and suburbanization of forests. To better understand the natural history of this secretive nesting species, we used both direct field observations and video cameras to study the nesting ecology of Broad-winged Hawks in three geographic regions of Pennsylvania, each with varying degrees of forest fragmentation. We recorded adult nest attendance, prey deliveries, and nest material deliveries from incubation through fledging. During 891 hr of observation during the nestling period, adult hawks were absent from the nest >72% of the time. Of the time at least one adult was present at the nest during the nestling stage, 77% was spent standing and sheltering, 21% feeding young, and 1% consuming food. Both adults were present at the nest <1% of the time. Mammals, birds, and reptiles and amphibians were the most frequently delivered prey items in that order, with the eastern chipmunk (*Tamias striatus*) composing >16% of the total prey delivered. Prey deliveries were more frequent during the first 3 wk of the nestling period than during the last 2 wk of the nestling period, but did not vary by time of day. The most frequently delivered nesting material was deciduous sprigs, which made up 55% of deliveries. Nest materials were delivered from incubation until the young were 4 wk old, but delivery rates varied significantly by nesting stage and nestling age. The absence of adults at the nests during nestling and fledgling periods may leave young vulnerable to predators. Although our sample size of nests in fragmented forests was too small for statistical analysis, the relationship between forest fragmentation and Broad-winged Hawk nesting ecology warrants further investigation.

KEY WORDS: *Broad-winged Hawk*; *Buteo platypterus*; *behavior*; *breeding*; *diet*; *nesting*; *nest material*; *observational study*.

COMPORTAMIENTO DE ANIDACIÓN DE *BUTEO PLATYPTERUS* EN PAISAJES BOSCOSOS DE PENNSYLVANIA

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RESUMEN.—Si bien *Buteo platypterus* se concentra en grandes números durante la migración, varias fuentes sugieren que sus poblaciones pueden estar disminuyendo regionalmente en el este de América del Norte, tal vez debido al aumento del desarrollo humano, la explotación de los recursos naturales y la sub-urbanización de los bosques. Para entender mejor la historia natural de esta especie con un modo de anidación poco conocido, usamos observaciones directas de campo y videocámaras para estudiar su ecología de anidación en tres regiones geográficas de Pensilvania, cada una con diferentes grados de fragmentación del bosque. Registramos la presencia de los adultos en el nido, las entregas de presas y las entregas de materiales de anidación desde la incubación hasta el emplumamiento. Durante 891 h de observación a lo largo de la etapa de polluelos, los adultos estuvieron ausentes del nido >72% del tiempo. Considerando el tiempo durante el cual al menos un adulto estuvo presente en el nido durante la etapa de polluelos, 77% se destinó a estar parado o protegiendo a los polluelos, 21% a alimentar a los polluelos y 1% a consumir alimentos. Ambos adultos estuvieron presentes en el nido <1% del tiempo. Los mamíferos, las aves, y los reptiles y anfibios fueron los ítems presa entregados con mayor frecuencia en ese orden, representando la ardilla *Tamias striatus* el >16% del total de las presas entregadas. La entrega de presas fue más frecuente durante las primeras tres semanas que durante las últimas dos semanas de la etapa de polluelos, sin mostrar variación según el momento del día. El material de anidación entregado con mayor frecuencia fue espigas deciduas que representaron hasta el 55% de las entregas. Los materiales de anidación fueron entregados desde la incubación hasta que los polluelos tuvieron cuatro semanas de edad, pero las tasas de entrega variaron significativamente según la etapa de anidación y la edad del polluelo. La ausencia de adultos en los nidos durante los períodos de polluelo y volantón puede dejar a los jóvenes vulnerables a los depredadores. Aunque nuestro tamaño de muestra de nidos en bosques fragmentados fue demasiado pequeño para analizarlo estadísticamente, la relación entre la fragmentación del bosque y la ecología de anidación de *B. platypterus* justifica una investigación más exhaustiva.

[Traducción del equipo editorial]

The Broad-winged Hawk (*Buteo platypterus*) is a common forest raptor that breeds across central and eastern North America. Large numbers of individuals migrate past hawk watch sites during the fall migration, with concentrations of >500,000 at sites in Texas, Mexico, and Central America (Inzunza et al. 2010, Goodrich et al. 2014). In spite of their abundance during migration, Broad-winged Hawk numbers declined significantly from 2004 to 2013 at four of nine eastern hawk watch sites in the Atlantic or Appalachian flyways (Brandes et al. 2013). In addition, Breeding Bird Surveys from 1996–2015 documented annual declines exceeding –1.5% in some northeastern states (Sauer et al. 2017). Of the 13 states in the northeast and mid-Atlantic, eight have designated the Broad-winged Hawk as a “Species of Greatest Conservation Need” (US Geological Survey 2015). Within one of those states, Pennsylvania, breeding bird atlas data showed a 16% decline in occupied atlas blocks from the first (1983–1989) to the second atlas (2004–2009), suggesting range retraction has occurred, particularly in southern counties (Brauning 1992, Wilson et al. 2012). The eastern US experienced a substantial and sustained net loss of forest (more than 3.70 million ha) and wetlands (over 273,000 ha) between 1973 and 2000 due to residential and urban expansion, mountaintop mining, timber harvesting, and clear-

cutting, resulting in a 4.1% decline in the total area of forest. Remaining forests have suffered fragmentation in some regions (Heimlich and Anderson 2001, Hall et al. 2002, Morrill 2006, Wickham et al. 2007, Drummond and Loveland 2010).

These changes, coupled with the Broad-winged Hawk’s preference for relatively large, contiguous forests in the eastern US (Titus and Mosher 1981, Goodrich et al. 2014), suggest reduction in forest extent could be affecting the species. Forest fragmentation could influence prey abundance and composition, as some prey species may increase (e.g., white-footed mice [*Peromyscus leucopus*]) while others may decrease (e.g., eastern chipmunk [*Tamias striatus*]; Nupp and Swihart 1998). Further, decreased forest cover reduces small mammal (Allan et al. 2003), bird, and amphibian populations (Robinson et al. 1995, Cushman 2006). Forest fragmentation also results in increased competition for nest sites or predation threats from larger raptors that prefer forest edges (e.g., Great Horned Owl [*Bubo virginianus*] and Red-tailed Hawk [*Buteo jamaicensis*]; Bosakowski and Smith 1997, Artuso et al. 2013). Many forests in the northeastern United States are even-aged and are losing some tree species, including the eastern hemlock (*Tsuga canadensis*) and ash (*Fraxinus* spp.) due to invasive insects (Allen and Sheehan 2010, Baiser et al. 2014).

Northeastern forests are also subject to over-browsing by white-tailed deer (*Odocoileus virginianus*), and other detrimental influences including residential and energy development, most of which exacerbate forest fragmentation (McWilliams et al. 2004, Allen and Sheehan 2010, Brittingham and Goodrich 2010, Stoleson and Larkin 2010).

Studies most likely to detect effects of fragmentation on wildlife are multi-year, landscape-scale investigations that examine functional traits, the latter defined as measurable characteristics of organisms with demonstrable links to the organism's fitness (Stephens et al. 2002, McGill et al. 2006, Vandewalle et al. 2010). By investigating specific nesting behaviors, including such functional traits as prey use and delivery rate over 2 yr, we provide empirical data on life-history traits that may be affected by fragmentation and may help elucidate causes of population declines. A better understanding of Broad-winged Hawks' nesting behavior may inform conservation management decisions.

The goals of this study were to: (1) compare Broad-winged Hawk nesting behaviors in three geographic regions with different patterns of forest cover; (2) determine the frequency of nesting behaviors (adult nest attendance, prey delivery, and nest material delivery) throughout the breeding season and; (3) summarize conservation implications of our results. We hypothesized that prey delivery rate and nest material delivery rate vary by time of day (with more deliveries in the morning than afternoon), and nestling age (with more deliveries during the first 4 wk than during the last 2 wk). We hypothesized that prey diversity and delivery rate may vary by region, and that adult attentiveness will decrease during the latter part of the nestling period, and may vary among regions, with less attendance in more fragmented regions, as prey may be more difficult to locate and parent hawks may encounter more disturbance.

METHODS

Study Sites. We studied Broad-winged Hawk ecology in three physiographic provinces in eastern Pennsylvania where forest landscapes differ: (1) the Ridge and Valley, 59% forested and characterized by continuous forest on linear ridges, with heavily fragmented agricultural or developed valleys, and where forest cover has remained stable from the 1990s to 2005; (2) the Piedmont, 32% forested and consisting of highly fragmented forests intermixed with suburban development, where forest cover

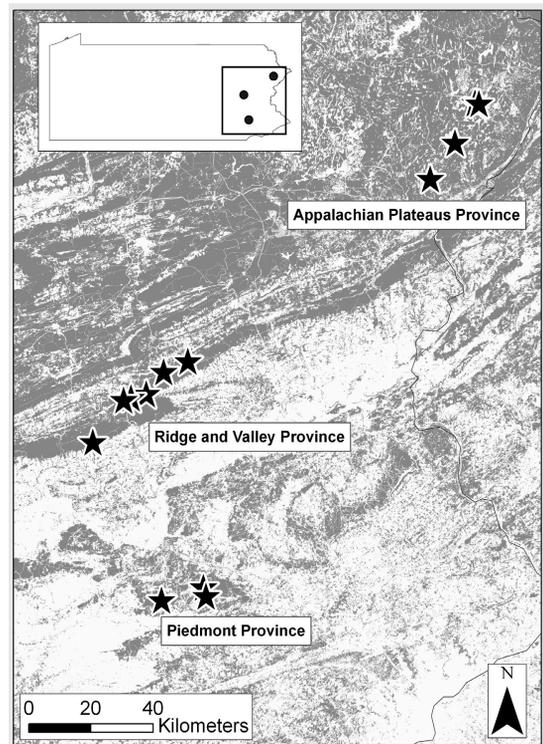


Figure 1. Broad-winged Hawk nests studied in three eastern Pennsylvania provinces (regions) during 2014–2015 ($n = 13$ nests). Gray represents forest cover and white represents non-forest cover.

declined by 6% from the 1990s to 2005; and (3) the Appalachian Plateaus, 71% forested with less-fragmented, mostly contiguous forest, and where forest cover has increased by 2.4% from 1990 to 2005 (Loucks et al. 1999, Department of Conservation and Natural Resources 2000, Wilson et al. 2012; Fig. 1). Study sites in the Ridge and Valley Province (RVP) were located within or near Hawk Mountain Sanctuary, a 1032-ha wildlife sanctuary on the Kittatinny Ridge in Berks and Schuylkill Counties ($40^{\circ} 77' N$, $75^{\circ} 59' W$). The physiographic section of the province in which the nest sites were located is characterized by linear ridges and valleys. In the Piedmont Province (PP), nest sites were located within or near the 3128-ha French Creek State Park in Chester and Berks Counties ($40^{\circ} 13' N$, $75^{\circ} 47' W$). Within the PP, nest sites were located in the Gettysburg-Newark Lowland section characterized by rolling lowlands, shallow valleys, and isolated hills. Broad-winged Hawk numbers declined in both the RVP and PP between the first and second Pennsylva-

nia breeding bird atlases (Wilson et al. 2012). The third province, the Appalachian Plateaus (APP), contained nests within or near Delaware State Forest (41° 14' N, 75° 9' W), a more extensive and less-fragmented 33,798-ha forest with remote bogs and glacial lakes characteristic of the Pocono region. Nests were located in the Glaciated Low Plateau, which is characterized by rounded hills and valleys.

The forests in all three ecoregions are dominated by oaks (northern red oak [*Quercus rubra*], white, black, and chestnut oaks [*Q. alba*, *Q. velutina* and *Q. prinus*, respectively]), red maple (*Acer rubrum*), and hickories (*Carya* spp.), with a coniferous component including white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*). During the breeding season (April–July), the mean temperature was 16.0°C in 2014 and 16.9°C in 2015, and the mean precipitation was 48.2 cm in 2014 and 48.6 cm in 2015 (National Oceanic and Atmospheric Administration 2016).

Nest Searches. Prior to the nesting season, we identified potential Broad-winged Hawk territories using reports from the *Second Atlas of Breeding Birds in Pennsylvania* (Wilson et al. 2012), eBird (Sullivan et al. 2014), the *Pennsylvania Birds* journal, or from Broad-winged Hawk nest locations and sightings reported by local birdwatchers. Historical nest sites and adult sightings also provided an initial starting point for nest searching. We created individual site maps for each potential nest territory in ArcMap (Environmental Systems Research Institute 2011), with GPS locations of historical observations for use by field assistants. Starting at known nest reference points, one or more individuals walked transects in a grid pattern, beginning in April, for an average of 2–4 hr every few days at each site, and ending in mid-May (during the hawks' incubation period). Field assistants recorded sightings, adults vocalizing or carrying nest material, and other behaviors. Sightings were mapped to better refine the search area. After we confirmed Broad-winged Hawk territories by observing 1–2 hawks in the area, we walked through the territory to locate stick nests in trees. Once a nest was found, we observed the nest from a distance of approximately 30–50 m to confirm it was being used by Broad-winged Hawks. We recorded the presence of fresh green sprigs or an adult in the nest as evidence of an occupied nest.

Field Observations. We conducted field observations during the incubation, nestling, and fledgling

stages between 19 May and 16 July 2014, and 20 May and 14 July 2015 at 11 territories in eastern Pennsylvania—four nests from RVP, three nests from the PP region, and four nests from APP. We defined the egg stage as the time from the beginning of incubation until hatching, the nestling stage as the time from when the first downy nestling was observed until fledging, and the fledgling stage as beginning when the first nestling began branching (perching on branches of the nest tree) and ending during the second week of July when observations ceased. Observation days were divided into four periods, each 3 hr in duration (Hengstenberg and Vilella 2004): (1) early morning (0700–1000 H); (2) late morning (1000–1300 H); (3) afternoon (1300–1600 H) and; (4) evening (1600–1900 H). We observed each nest at least twice per week during one morning and one afternoon/evening session, with nest, time period, and observer randomly assigned each day to eliminate potential bias. Observers viewed nests with a 20–60× spotting scope and binoculars from behind camouflaged netting at a distance of at least 50 m, and recorded prey deliveries, nest-material deliveries, and adult behaviors.

We classified adult behaviors as incubating, standing and sheltering, feeding young, or consuming food. We defined “standing and sheltering” to include standing when delivering nest materials and prey prior to feeding, as well as sheltering young (brooding) from natural elements or predators (combined as a single behavior category). We also recorded all time that both adults were present in the nest together. For both direct observations and camera recordings, we defined nest attendance as the presence of one or both adults in the nest, on the nest edge, or in the branches above the nest. We recorded adult behaviors to the nearest minute, except in the case of both adults at the nest, which was recorded to the nearest second.

We recorded prey deliveries and identified prey items to family, genus, or species level, if possible. We calculated biomass by multiplying the number of individuals of each prey type by the mean mass of that species (Marti et al. 2007), using weights from Steenhof (1983) and Reid (2006). We removed insects and unknown prey items from prey analysis because of the low number of insect deliveries recorded.

We recorded nest material deliveries and identified items to family, genus, or species level, if possible. We lumped lichen, fresh sprigs unknown,

and unknown into an “other” category due to the low number of deliveries recorded.

Nest Cameras. Two high-resolution weatherproof cameras (Backstreet Surveillance, Salt Lake City, Utah, USA) were installed in 2014 at two territories in the RVP region. Cameras were installed after hatching to minimize nest disturbance during incubation. We only considered nests near roads and within a 30-min drive of Hawk Mountain as logistically suitable for camera installation. We used bucket trucks to install each nest camera approximately 2 m above each nest; the field of view for each included the entire nest and nearby surroundings. We recorded video at nests from 0600–1900 H daily from 24 June to 20 July in 2014. We later watched the recordings to document adult behavior, prey deliveries, and nest material deliveries for the morning and afternoon time periods. We compared data extracted from every other day of recorded video and compared metrics associated with adult behavior to the entire dataset to determine if there were significant differences in the rates and frequencies of behaviors recorded. Because we found no differences (two sample *t*-test, $P > 0.05$), we reduced the sampling time to every other day after the third week post-hatching.

Data Analysis. We examined two sets of behavioral data in this study: (1) descriptive analysis of pooled field and camera observations for both years ($n = 13$ territories; two nests with camera observation and 11 nests with field observations; and (2) field observations only ($n = 11$ nests, 11 territories). For the purpose of this analysis, we did not include direct field observations for one nest that had both camera and direct field observations being recorded simultaneously in the same season. For nest territories where we recorded data in two years, we included only one season of data in our analysis.

We compared behaviors among daytime observation periods and over time as the nestlings aged using general linear mixed models (GLMMs). We used the 3-hr observation periods as our sampling unit, and included both year and nest site as random effects in the mixed models. We divided the observations during the nestling phase by week, with week 1 = day 0–day 6, where day 0 was defined as the first day a nestling was observed in the nest. We only examined field observations for these comparisons. We used Tukey’s Honest Significant Differences (HSD) to compare behavior frequency per hour of observation (e.g., prey deliveries/hr, nest material deliveries/hr, and adult attendance in

min/hr of observation) among daytime observation periods, nesting stages, and nestling age.

We conducted all statistical analyses in SYSTAT (2009). The alpha level for all tests was 0.05.

RESULTS

In 2014 and 2015 we observed Broad-winged Hawk nests ($n = 11$ nests) for a total of 791 hr: 225 hr during the incubation stage, 491 hr during the nestling stage, and 75 hr during the fledgling stage. We viewed 566 hr of camera recordings ($n = 2$ nests) in 2014: 0 hr during incubation, 400 hr during the nestling stage and 166 hr during the fledgling stage. At the 13 nests monitored, a total of 23 of 29 juveniles survived; one nest in the PP region failed during the nestling phase, and one nest in APP and one nest in RVP had nestlings die post-fledging (e.g., nestlings found dead in nest or at the base of the nest tree, R. McCabe unpubl. data).

Regions with general differences in levels of forest fragmentation and composition qualitatively showed no difference in deliveries and behavior (McCabe 2016). For field observations only, we compared adult attendance among the three geographic regions and found no significant difference among regions ($P > 0.05$); we were unable to compare prey deliveries and nest material deliveries by regions because sample sizes were too small. Thus, we pooled all regions for subsequent analyses.

Nest Attendance. During the 1357 hr of observation between 0600–1900 H (camera and field observations pooled for two nesting seasons, $n = 13$ nests), at least one adult was present at the nest 27% of the time during the nestling stage (237 hr out of 891 hr of nestling-stage observations). Of the time an adult was present at the nest during the nestling stage, 77% was spent standing and sheltering, 21% feeding young, 1% consuming food. Both adults were present together <1% of the time, on 81 occasions for 33 min total during all 2014 and 2015 observations ($n = 13$ nests), with an average of 12 sec per joint visit.

Adult nest attendance did not vary among the four daytime periods during field observations across the two seasons ($n = 11$ nests; $F_{3,290} = 1.17$, $P = 0.32$). Adult attendance at the nest varied significantly among incubation, nestling, and fledgling nesting stages. Adults spent significantly more time at the nest during incubation ($\bar{x} = 53.2$ min/hr; 88% of the time) compared to the nestling stage ($\bar{x} = 18.31$

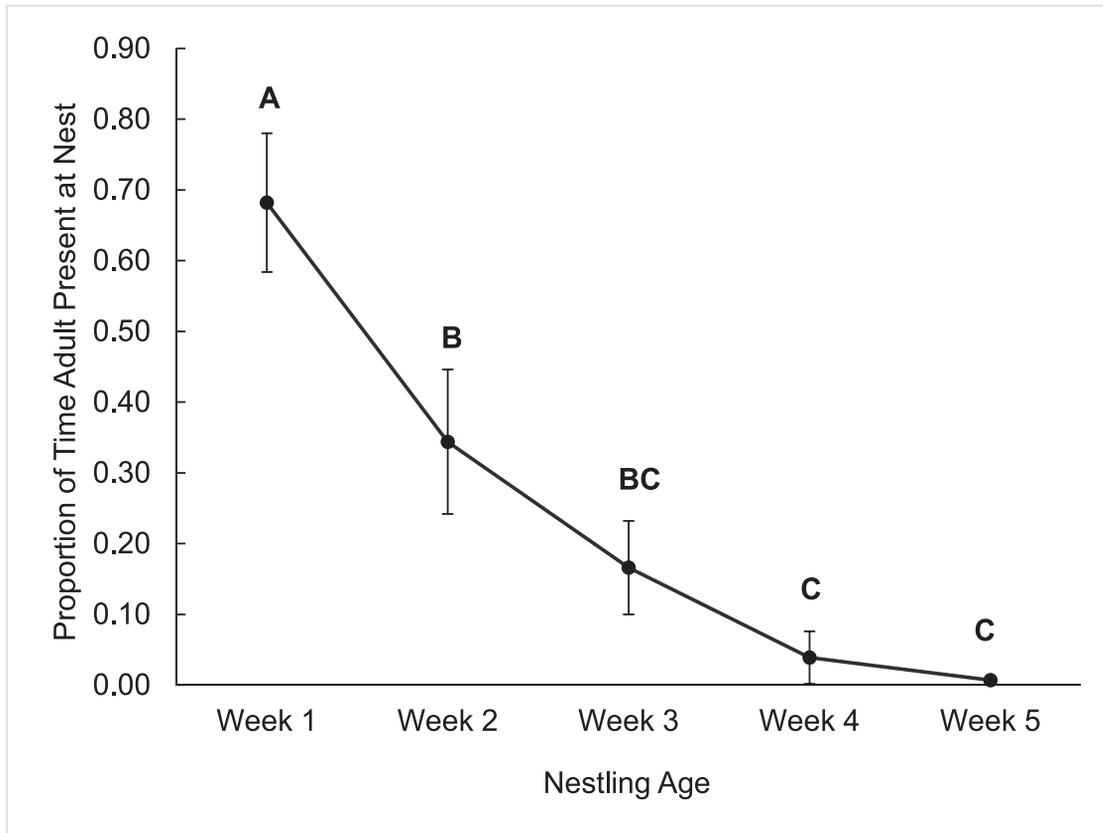


Figure 2. Mean proportion of time at least one adult Broad-winged Hawk was present at the nest throughout the nestling period ($n = 11$ nests) in Pennsylvania in 2014–2015. Error bars represent SE. Means with different letters differed significantly ($P < 0.05$), based on Tukey's post hoc test.

min/hr; 30% of the time) and fledgling stage ($\bar{x} = 0.53$ min/hr; 1% of the time), and more time at the nest during the nestling stage compared to fledgling stage ($n = 11$ nests; $F_{2,290} = 107.41$, $P = 0.0001$; Tukey's HSD incubation to nestling: $t = 12.591$, $P = 0.0001$; incubation to fledgling: $t = 11.985$, $P = 0.0001$; nestling to fledgling: $t = 4.449$, $P = 0.001$). Adult attendance also decreased as nestlings aged ($n = 11$ nests; $F_{4,36} = 17.439$, $P = 0.0001$; HSD week 1 vs. week 2: $t = 3.812$, $P = 0.004$; week 1 vs. week 3: $t = 5.824$, $P = 0.0001$; week 1 vs. week 4: $t = 6.749$, $P = 0.0001$; week 1 vs. week 5: $t = 7.018$, $P = 0.0001$; week 2 vs. week 4: $t = 3.162$, $P = 0.025$; week 2 vs. week 5: $t = 3.430$, $P = 0.012$; Fig. 2).

Prey Deliveries. Of the 425 prey items delivered to Broad-winged Hawk territories ($n = 13$ nests), we were unable to identify 32% of the prey items for the following reasons: (1) the vegetation obstructed view

of the delivery, (2) the birds' body positions when feeding blocked the view of the prey or, (3) the prey was too small to identify. Of the 68% that we were able to identify, mammals made up more than one-third of the prey delivered (38%), followed by birds (18%), reptiles and amphibians (11%), and insects (~1%; Table 1). The most frequent prey item observed was the eastern chipmunk, composing >16% of the total prey delivered and accounting for >62% of the total biomass.

After the removal of unknowns and insects, we found no significant differences in proportions of the three most common prey types (mammals, birds, and reptiles and amphibians) among the three nesting stages (incubation, nestling, and fledgling; $\chi^2 = 4.209$, $df = 4$, $P = 0.378$), or by nestling age ($\chi^2 = 13.821$, $df = 16$, $P = 0.612$; Fig. 3). Prey delivery rates also did not differ among the four observation time

Table 1. Prey items ($n = 425$) delivered by Broad-winged Hawks to 13 nests in Pennsylvania, USA, during 2014–2015.

PREY TYPE	NUMBER (% OF TOTAL)	MASS (g) ^a	BIOMASS (% OF TOTAL)
Mammals (total)	162 (38.1)	(6–340)	
Eastern chipmunk (<i>Tamias striatus</i>)	70 (16.5)	106.5	62.7
Unidentified small mammal	62 (14.6)	-	-
Muridae spp.	11 (2.6)	184	17.0
Short-tailed shrew (<i>Blarina brevicauda</i>)	10 (2.4)	17	1.4
Eastern cottontail (<i>Sylvilagus floridanus</i>), assumed to be juv.	3 (0.7)	100	2.5
Cricetidae spp.	2 (0.5)	40.5	0.7
Star-nosed mole (<i>Condylura cristata</i>)	1 (0.2)	53.5	0.4
Talpidae spp.	1 (0.2)	96	0.8
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	1 (0.2)	226	1.9
Sciuridae spp.	1 (0.2)	198	1.7
Birds (total)	78 (18.4)	(5–140)	
Unidentified bird, assumed to be passerine	65 (15.3)	-	-
Unidentified nestling	6 (1.4)	-	-
Downy Woodpecker (<i>Picoides pubescens</i>)	3 (0.7)	24.5	0.6
Picidae spp.	1 (0.2)	58	0.5
Passeridae spp.	1 (0.2)	30	0.3
Turdidae spp.	1 (0.2)	100	0.8
Indigo Bunting (<i>Passerina cyanea</i>)	1 (0.2)	15	0.1
Reptiles and Amphibians (total)	45 (10.6)	(5–500)	
Unidentified reptile	25 (5.9)	-	-
Ring-necked snake (<i>Diadophis punctatus</i>)	2 (0.5)	22.5	0.4
Common garter snake (<i>Thamnophis sirtalis</i>)	2 (0.5)	125	2.1
Eastern milk snake (<i>Lampropeltis triangulum</i>)	1 (0.2)	385	3.2
Unidentified amphibian	11 (2.6)	-	-
Ranidae spp.	1 (0.2)	270	2.3
Plethodontidae spp.	1 (0.2)	6.5	0.1
Green frog (<i>Lithobates clamitans</i>)	1 (0.2)	53.5	0.4
Wood frog (<i>Lithobates sylvaticus</i>)	1 (0.2)	8	0.1
Insects (total)	5 (1.2)	(<1–3)	
Unidentified insect	2 (0.5)	-	-
Hymenoptera spp.	1 (0.2)	-	-
Unidentified caterpillar	1 (0.2)	-	-
Unidentified grub/larvae	1 (0.2)	-	-
Unknown prey	135 (31.8)		

^a Prey weight (Steenhof 1983 and Reid 2006) reported as median from range of low to high weights per species.

periods ($n = 11$ nests; $F_{3,291} = 1.387$, $P = 0.247$; field observations only). Prey delivery rates varied significantly among the nesting stages, with fewer deliveries during the incubation stage compared to nestling and fledgling stages ($n = 11$ nests; $F_{2,292} = 13.304$, $P = 0.0001$); Tukey’s HSD incubation to nestling: $t = 4.964$, $P = 0.0001$, incubation to fledgling: $t = 3.325$, $P = 0.003$; Fig. 4). Prey delivery rate by nestling age was similar in most weeks, except that week 3 had significantly more deliveries than week 5 ($n = 11$ nests; $F_{6,239} = 3.681$, $P = 0.002$; HSD week 3 vs. week 5: $t = 3.454$, $P = 0.010$; Fig. 5).

Nest Material Delivery. Adult hawks delivered five identifiable nest material types during the incubation, nestling, and fledgling periods ($n = 271$ deliveries in 13 territories): (1) bark, (2) dead sticks, (3) fresh coniferous sprigs, (4) fresh deciduous sprigs, or (5) other items, which included lichen, fresh unknown sprigs, and other unknown materials (Table 2). Fresh deciduous sprigs made up 55% of all nest material delivered. Dead sticks made up 22%, bark 11%, fresh coniferous sprigs 7%, and other items 5%.

We examined nest material types by nesting stage and across the nestling period using field observa-

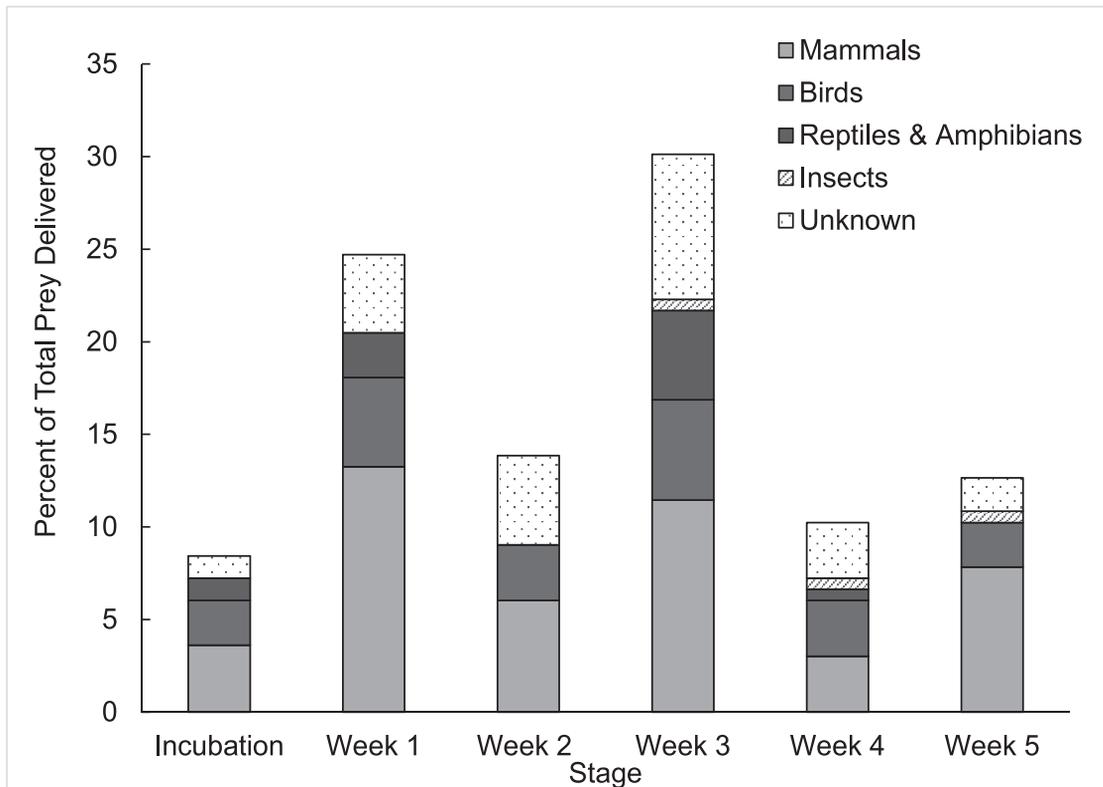


Figure 3. Prey types delivered to 11 Broad-winged Hawk nests in Pennsylvania, 2014–2015, during the incubation stage, and week 1–week 5 of the nestling stage. Insects and unknown prey items were excluded from statistical analysis but shown here for comparison.

tions only. After the removal of the items in the other category, we found that adults delivered dead sticks more frequently during the incubation stage and fresh deciduous sprigs more frequently during the nestling stage ($\chi^2 = 21.913$, $df = 3$, $P = 0.001$). Nest material types delivered did not vary with nestling age ($\chi^2 = 8.119$, $df = 6$, $P = 0.229$; Fig. 6).

Nest material delivery rates did not differ by daytime observation period during field observations ($n = 11$ nests; $F_{4,292} = 1.99$, $P = 0.095$). However, mean nest material delivery rate varied significantly by nesting stage, with the fledgling stage having zero nest material deliveries compared to egg ($\bar{x} = 0.52 \pm 0.07$ per 3-hr observation period) and nestling stages ($\bar{x} = 0.38 \pm 0.04$ per 3-hr observation period; $F_{2,294} = 7.053$, $P = 0.001$; Tukey's HSD incubation vs. fledgling: $t = 3.646$, $P = 0.001$, nestling vs. fledgling: $t = 2.807$, $P = 0.014$). Nest material delivery rates differed by nestling age, with more deliveries during week 1 and week 2, and none in week 5 ($n = 11$ nests;

$F_{2,200} = 6.741$, $P = 0.0001$; HSD week 1 vs. week 3: $t = 2.723$, $P = 0.05$; week 1 vs. week 5: $t = 3.072$, $P = 0.018$; week 2 vs. week 3: $t = 4.028$, $P = 0.001$; week 2 vs. week 4: $t = 2.865$, $P = 0.034$; week 2 vs. week 5: $t = 3.980$, $P = 0.001$; Fig. 7).

DISCUSSION

Broad-winged Hawks showed consistent behavior among forested regions in Pennsylvania, delivering a wide variety of prey and nest materials to the nest, with fewer deliveries late in the nestling period. Adult nest attendance decreased from week 1 to week 5 of the nestling period, with an overall attendance of 27% during the nestling period. During our field observations, both adults were absent 11% of the time during the incubation stage, 70% during the nestling stage, and 99% of the time during the fledgling stage. Similarly, adult Broad-winged Hawks in Puerto Rico were absent from the nest 15% of the time during incubation and 69% of

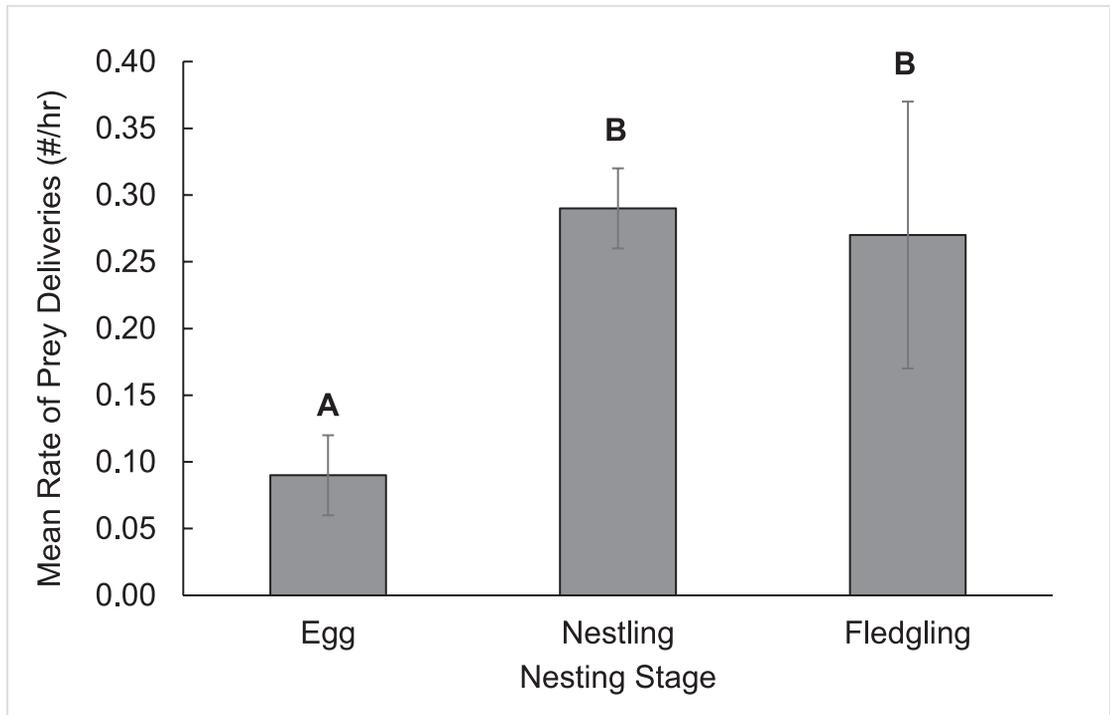


Figure 4. Broad-winged Hawk prey delivery rate (mean \pm standard error) by nesting stage ($n = 11$ nests) at Pennsylvania nests in 2014–2015. Prey deliveries were less frequent during incubation compared to nestling and fledgling stages. Means with different letters differed significantly ($P < 0.05$), based on Tukey’s post hoc test.

the time during the nestling period (Hengstenberg and Vilella 2004). As nestlings matured and improved in their ability to thermoregulate and feed themselves, Broad-winged Hawk adult nest attendance decreased, in our study and elsewhere (Matray 1974, Lyons and Mosher 1987, Hengstenberg and Vilella 2004). Parental time allocation influences nest survival and success in other species (Williams 1966, Martins and Wright 1993), and parental presence at the nest may be an important factor in dissuading predators and protecting young from inclement weather (Montgomerie and Weatherhead 1988). Nestlings left unattended can fall victim to predators, but well-camouflaged nests may provide partial protection and allow safe foraging time for parents. An observation of low nest attendance by adults during the nestling stage might suggest that the demand for foraging outweighs nest attendance as a priority, and finding prey may be difficult. However, the comparison of adult attendance at our study area to that documented in Puerto Rico suggests that adult attendance in Pennsylvania was typical, and nest success in our

study was 92% (McCabe 2016), greater than that of Broad-winged Hawk nests in Ontario (88%; Armstrong and Euler 1983) and Wisconsin (79%; Rosenfield 1984). The likely cause of the rare occurrence of nestling mortality from our nest sites was predation, and in one case nestlings were found dead at the base of the nest tree suggesting prey contamination or starvation (R. McCabe unpubl. data). During the nest-searching period of this study, we did locate nests that subsequently failed during incubation and were not included in this study; thus our success rate is not completely comparable to those documented elsewhere. Predation may be a more important factor limiting Broad-winged Hawk nesting success and distribution than prey availability given the wide array of prey used by this species. However, more research is needed to understand patterns of nest success in varied landscapes.

Only two previous studies have reported on nest attendance at Broad-winged Hawk nests. Matray (1974) observed a clear division of labor, with females performing most incubation and brooding of nestlings. Males provided food for both incubat-

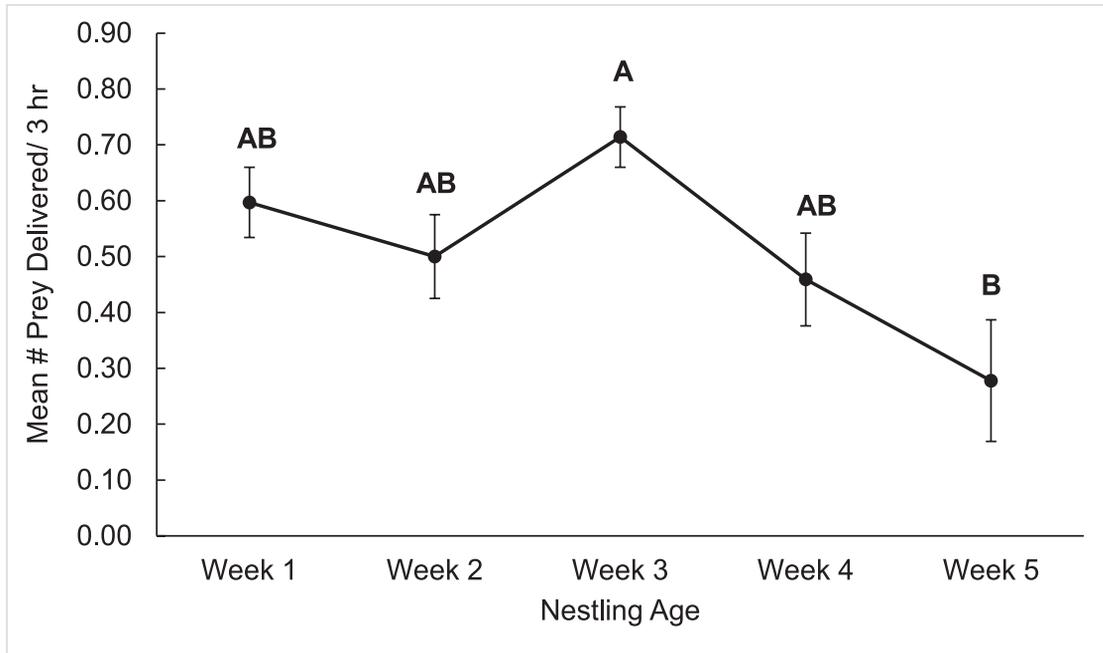


Figure 5. Mean number of prey delivered per 3-hr observation period during the nestling stage to 11 Broad-winged Hawk nests in Pennsylvania (2014–2015) throughout the nestling period. Error bars represent SE. Means with different letters differed significantly ($P < 0.05$), based on Tukey’s post hoc test.

ing females and nestlings during short and infrequent visits. The same pattern was noted in Maryland, where visits by the males to the nest never exceeded 3 min (Lyons and Mosher 1987). Standing

Table 2. Nest materials ($n = 271$) delivered by Broad-winged Hawk to 13 nests in Pennsylvania, USA, during 2014–2015.

NEST MATERIAL TYPE	NUMBER (%)
Fresh deciduous sprig	149 (55.0)
<i>Quercus</i> spp.	38 (14.0)
White oak (<i>Quercus alba</i>)	6 (2.2)
<i>Prunus</i> spp.	6 (2.2)
<i>Acer</i> spp.	5 (1.8)
Red maple (<i>Acer rubrum</i>)	1 (0.4)
<i>Betula</i> spp.	1 (0.4)
Unidentified deciduous	92 (34.0)
Dead sticks	59 (21.8)
Bark	31 (11.4)
Fresh coniferous sprig	19 (7.0)
Canada hemlock (<i>Tsuga canadensis</i>)	16 (5.9)
Eastern white pine (<i>Pinus strobus</i>)	1 (0.4)
Unidentified conifer	2 (0.7)
Other (lichen, fresh sprigs unknown, and unknown)	13 (4.8)

and sheltering behaviors and the consumption of food were not specifically discussed in detail in previous studies, but our results showed that adults consume food when present at the nest and spend notable amounts of time at the nest during the first few weeks of the nestling stage. Matray (1974) noted that female nest-attendance bouts ranged from a few seconds to >8 hr during the incubation and nestling stages. Other researchers report that female Northern Goshawks (*Accipiter gentilis*) occasionally stand on the rim of the nest to stretch and preen or intermittently feed themselves while feeding offspring (Schnell 1958). In our study, females were responsible for incubating, brooding, and feeding young (R. McCabe unpubl. data), as noted by other observers (Matray 1974, Lyons and Mosher 1987). The presence of both adults at the nest was a rare event; most joint visits lasted <1 min. Males brought most food into nests during our study, but females almost always fed the young (R. McCabe unpubl. data), a division of parental roles similar to that seen in Golden Eagles (*Aquila chrysaetos*; Collopy 1984) and other raptors.

Prey use by nesting raptors can be influenced by a variety of factors including prey abundance cycles

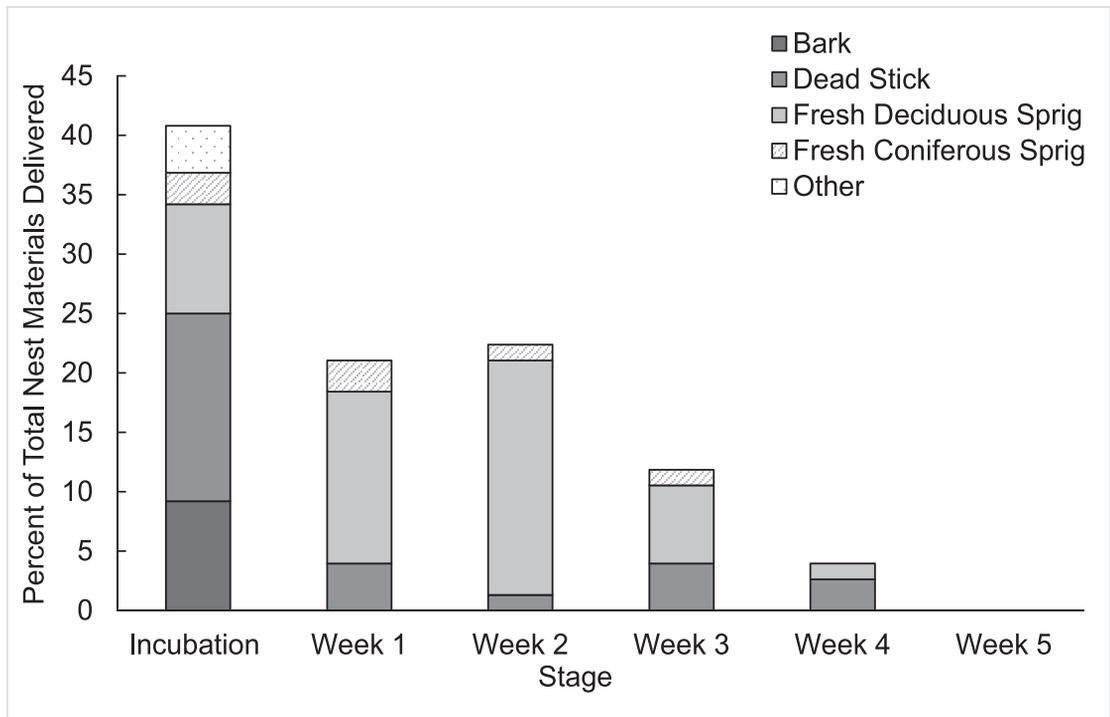


Figure 6. Types of nest materials delivered to 11 Broad-winged Hawk nests in Pennsylvania (2014–2015) during incubation, and week 1–week 5 of the nestling stage.

(Gilg et al. 2003, Therrien et al. 2014), weather or environmental effects on prey abundance and availability (Steenhof et al. 1997, Dawson and Bortolotti 2000), human disturbance, and competition for prey with other predators (Steenhof and Kochert 1985, 1988). Percentages of birds and mammals delivered by Broad-winged Hawks in our study were generally similar to those in Wisconsin (Rosenfield et al. 1984) and New York (Crocoll 1984): 40–46% mammals, and 26–28% birds. The percentage of reptiles and amphibians reported in both those studies, 28–31%, was more than double that documented in our study. The smaller percentage of herpetofauna in the Broad-winged Hawk diet in Pennsylvania may be linked to the global amphibian declines caused by land-use change, disease, and climate change (Cushman 2006, Adams et al. 2013). The smaller proportions of birds, reptiles, and amphibians brought to the nest compare similarly with studies in Alberta, New York, and Wisconsin (Rusch and Doerr 1972, Mosher and Matray 1974, Janik and Mosher 1982, Rosenfield et al. 1984). Fitch (1974) observed three nests in

Kansas and found birds were the primary prey, with fewer mammals, and few reptiles and amphibians, whereas the latter were identified as major prey items in Maryland (Mosher and Matray 1974). The Broad-winged Hawk’s diet was dominated by small mammals, particularly the eastern chipmunk, which was the most frequently delivered mammal species in Pennsylvania and western Maryland (Janik and Mosher 1982). The abundance of eastern chipmunks in the diet confirms the importance of this prey species to nestlings in terms of both the number delivered and biomass necessary to satisfy daily energy expenditure (Mosher and Matray 1974, Steenhof 1983, Bozinovic and Medel 1988). Prey use may also be influenced by forest fragmentation (Nupp and Swihart 1998, Allan et al. 2003); eastern chipmunks are largely intolerant of non-forested habitat (Snyder 1982, Bennett et al. 1994), exhibit lower survival rates in woodlots, and are negatively affected by fragmentation (Nupp and Swihart 1998).

The prey items documented in this study confirm that Broad-winged Hawks are generalist predators, a trait that allows them to exploit a variety of forest

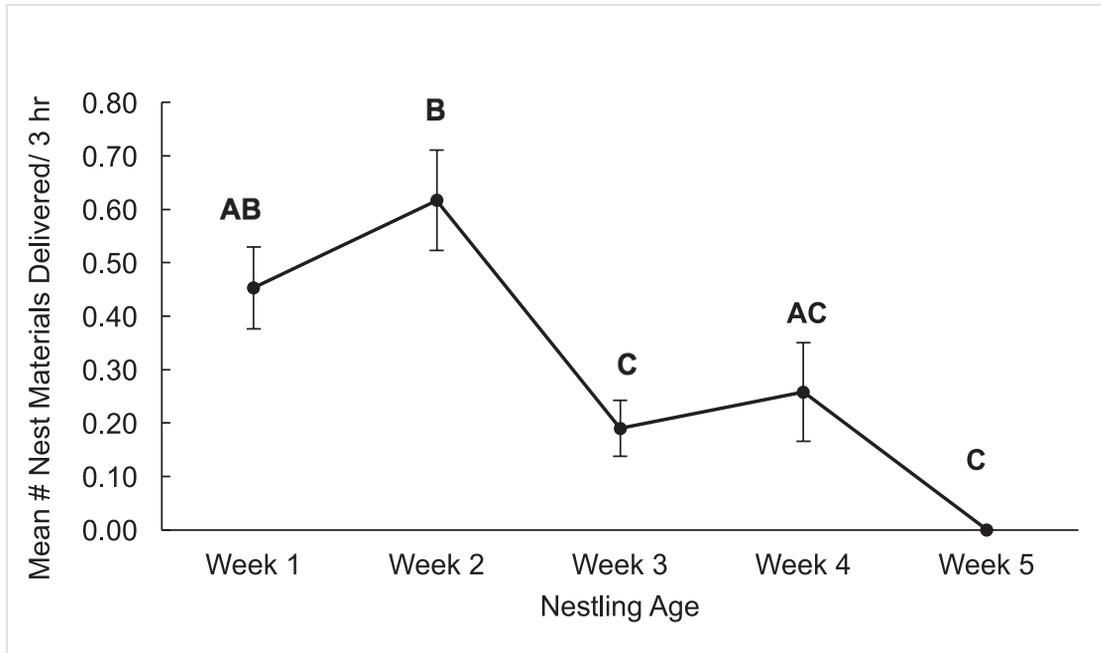


Figure 7. Mean number of nest materials delivered during 3-hr observation periods to 11 Broad-winged Hawk nests in Pennsylvania (2014–2015) throughout the nestling period. Error bars represent SE. Means with different letters differed significantly ($P < 0.05$), based on Tukey's post hoc test following GLMM with nest site and year as random effect.

types. Adult birds may respond to local prey availability within their range, allowing for greater flexibility and adaptation to prey abundance and availability through the nesting season (Crocoll 1984). Steblein (1991) suggested Broad-winged Hawks select foraging sites with high prey availability, such as mature to old-growth forests, or along small openings such as forest roads and streams. As one of the major threats to Broad-winged Hawks, habitat loss or degradation can decrease availability and/or diversity of prey, reduce nesting success, and ultimately reduce populations (Reynolds 1983, Robinson et al. 1995).

We did not find a difference in the prey delivery rates among daytime observation periods, whereas prey deliveries to nestlings in Puerto Rico occurred mainly between 0800 and 1400 H (Hengstenberg and Vilella 2004). Fitch (1974) calculated an average of 1.28–2.71 prey items delivered per day, with deliveries increasing as the day progressed and most frequent during the second week of the nestling stage. The differences in delivery rates among the three studies may reflect differences in prey activity patterns or prey abundance in different forested regions. In Pennsylvania, the wide variety of prey

brought to nests may contribute to consistency in delivery rates throughout the day.

Prey delivery rates were significantly lower during incubation compared to the nestling and fledgling stages during our field observations. This corresponds to other sources documenting parental behavior (Newton 1979, Slagsvold and Sonerud 2007, Sonerud et al. 2014).

Fewer studies have reported on nest material delivery. Nest material, or more specifically fresh green sprigs brought to the nest, is thought to have many functions including repelling ectoparasites (Clark and Mason 1984, Wimberger 1984), consolidating nest structure (Lyons et al. 1986), increasing nest longevity in a tree (Newton 1979), or serving a nest-sanitation function (Heinrich 2013). Broad-winged Hawks in Pennsylvania used a variety of twigs, sticks, and plant material to construct nests, including regular and characteristic additions of fresh green sprigs, leaves, and sometimes tree blossoms (Burns 1911). In New York, females in particular brought bark strips to the nest and both adults brought living sprigs from various tree species (Matray 1974). Fresh sprigs from six tree species were recorded at most nests in a Maryland study that

also addressed placement, timing, and frequency of sprig delivery (Lyons et al. 1986). Adults in Maine delivered green sprigs from ten plant species including five species of ferns (Heinrich 2013). Heinrich (2013) also distinguished between sprigs added onto the nest and those added to the nest lining post-hatching, the latter likely playing a role in nest hygiene. Adults from our study delivered nest materials consisting mostly of fresh deciduous sprigs and dead sticks. The fresh deciduous sprigs came from oaks and maples (Table 2), tree species common within their nesting habitat (McCabe 2016), suggesting that Broad-winged Hawks may use nest material in proportion to availability within their territory. Dead sticks delivered during the incubation stage are probably used to shore up the nest structure and prepare for the transition to fresh deciduous sprig delivery post-hatching (Rosenfield 1982, Lyons et al. 1986, Heinrich 2013). Further investigation is necessary to understand the purpose of fresh sprig delivery.

We found nest material delivery rates and types varied among pairs (R. McCabe unpubl. data). Although not quantified, our camera recordings revealed a pattern of fresh sprig delivery to the nest just after adults fed young (R. McCabe unpubl. data), which could support the hypothesis that volatile compounds in fresh sprigs help reduce insect numbers at the nest (McDonald et al. 1995). Broad-winged Hawks at one nest site in western Maine averaged two nest material deliveries per day during the first 18 d post-hatching, followed by one per day for the last 17 d the young were in the nest (Heinrich 2013), similar to our results of 1–2 deliveries per day during incubation and early nestling stages vs. 0–1 deliveries per day during late nestling and early fledgling stages.

The relative abundance of the Broad-winged Hawk in northeastern forests contrasts with how little is known about their nesting behavior. By focusing our research in Pennsylvania regions where Broad-winged Hawk nesting has declined, we were able to illuminate potential advantages and disadvantages (vulnerabilities) that behaviors confer in the face of habitat fragmentation. Our study can thus inform conservation and management efforts to protect this species, its habitat, and the resources it requires. For example, dietary variety would seem to be an advantage, but the time spent foraging away from the nest can leave nest sites vulnerable to predators, particularly in regions where numbers of nest predators such as Great Horned Owls are enhanced

through forest fragmentation (Grossman et al. 2008, Artuso et al. 2013, Goodrich et al. 2014). Our study complements the few other studies reporting on nest observations and provides baseline data for this species for comparison to other at-risk populations or for future investigations on the effects of climate change and landscape changes on behavior and reproduction.

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