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CAUSES OF MORTALITY AND FAILURE AT SUBURBAN RED-SHOULDERED HAWK (*BUTEO LINEATUS*) NESTS¹

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ABSTRACT.—There have been no detailed studies of predator or non-predator causes of mortality and failure at nests of the Red-shouldered Hawk (*Buteo lineatus*), and identification of such causes has been largely speculative. There is ample information about rates of nest success, defined as the fledging of ≥ 1 nestling from a nest, but this measure of reproductive rate is limited in its scope. Fledging success, measured by quantifying total nestlings lost or fledged is a more informative assessment of reproductive success, but is not often reported. We used video monitoring of suburban Red-shouldered Hawk nests to identify causes of mortality or failure. Eight of 25 nests failed completely (32%), and 17 were successful (68%). However, nine of the 17 successful nests experienced some nestling mortality, and the fledging success of individual nestlings ($n = 67$) was only 58%, as 28 nestlings (42%) died before fledging. Causes of mortality or nest failure included depredation of an incubating female parent at one nest and of nestlings at multiple nests by Great Horned Owls (*Bubo virginianus*), depredation of nestlings by raccoons (*Procyon lotor*), disturbance by eastern gray squirrels (*Sciurus carolinensis*), unexplained disappearance of female parents, starvation of nestlings, and nestlings falling from the nest. These results provide a thorough and accurate account of reproductive success, and valuable identification of predator and non-predator causes of nestling mortality or nest failure throughout the nesting period.

KEY WORDS: Red-shouldered Hawk; *Buteo lineatus*; breeding; nest success; predator; reproductive rate; video monitoring.

CAUSAS DE MORTALIDAD Y FRACASO EN NIDOS SUBURBANOS DE *BUTEO LINEATUS*

RESUMEN.—No hay estudios detallados de las causas de mortalidad y fracaso de nidos de *Buteo lineatus* ocasionadas o no por depredadores y la identificación de tales causas ha sido en gran medida especulativa. Existe mucha información sobre las tasas del éxito de nidificación, definido como el abandono del nido de uno o más pollos volanderos. Sin embargo, esta medida de la tasa reproductiva tiene un alcance limitado. La tasa de vuelo, medida como el total de pollos perdidos o que dejaron el nido, proporciona una mejor estima del éxito reproductivo, pero a menudo no es mostrada. Monitoreamos con cámaras de video nidos suburbanos de individuos de *B. lineatus* para identificar las causas de mortalidad o fracaso. Ocho de 25 nidos fracasaron completamente (32%) y 17 tuvieron éxito (68%). Sin embargo, nueve de los 17 nidos exitosos experimentaron algún grado de mortalidad de pollos y la tasa de vuelo de pollos individuales (n

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= 67) fue sólo del 58%, ya que 28 pollos (42%) murieron antes de dejar el nido. Las causas de mortalidad o de fracaso del nido incluyeron la depredación de una hembra progenitora en un nido y de pollos en múltiples nidos por parte de *Bubo virginianus*, la depredación de pollos por parte de *Procyon lotor*, molestias causados por *Sciurus carolinensis*, desaparición sin explicación de hembras progenitoras, muerte por inanición y caída de pollos del nido. Estos resultados proporcionan una explicación detallada y precisa del éxito reproductivo y aportan información valiosa sobre la identificación de las causas de mortalidad de los pollos o el fracaso del nido a lo largo del periodo de nidificación.

[Traducción del equipo editorial]

In the eastern U.S., Red-shouldered Hawks (*Buteo lineatus*) primarily utilize habitat with extensive mature, mixed deciduous-coniferous forests, particularly riparian and bottomland hardwood areas, and flooded deciduous swamps (Bednarz and Dinsmore 1982, Morris and Lemon 1983, Woodrey 1986, Howell and Chapman 1997). In some parts of its eastern and Californian ranges, including in southern Ohio, this species is fairly common in suburban and residential areas that are partially forested or adjacent to intact forests (Bloom and McCrary 1996, Dykstra et al. 2000, Rottenborn 2000). In southern Ohio, Red-shouldered Hawks begin courtship in mid-January, with egg-laying commencing in late March (Dykstra et al. 2008). Clutch size typically ranges from 2–4 eggs (Portnoy and Dodge 1979, Townsend 2006, Miller 2013), incubation lasts about 33 d per egg (Palmer 1988, Miller 2013), and young fledge in 6–7 wk (Wiley 1975a, Portnoy and Dodge 1979, Penak 1982, Crocoll and Parker 1989).

Nest predation is a commonly reported cause of nestling mortality and nest failure for the Red-shouldered Hawk. Great Horned Owls (*Bubo virginianus*) are one of the most frequent predators of Red-shouldered Hawk nests, depredating both nestlings and adults (Craighead and Craighead 1956, Wiley 1975b, Portnoy and Dodge 1979, Crocoll and Parker 1989, Martin 2004). Red-tailed Hawks (*Buteo jamaicensis*) are both potential nest predators and possible competitors for nest sites (Campbell 1975, Martin 2004), as their territories are often adjacent or overlapping with those of Red-shouldered Hawks in the study area (S. Miller and C. Dykstra unpubl. data). Raccoons (*Procyon lotor*) are also known predators at bird nests, including those of Red-shouldered Hawks (Craighead and Craighead 1956, Bednarz 1979). Nestling mortality in this species has also been caused by falls from the nest, resulting from stormy weather (Wiley 1975a, Portnoy and Dodge 1979, Dijak et al. 1990) or a physical competition with siblings (Townsend 2006). Nestling mortality due to starvation has been observed in Red-

shouldered Hawks (Crocoll and Parker 1989, Miller 2013), and has been proposed as a means of brood reduction in birds during times of low food availability (Lack 1947, 1954). It is also possible that nestlings may die as the result of infanticide or siblicide, including in circumstances where smaller offspring serve as an extra food source for surviving siblings, as proposed by Alexander's (1974) "icebox hypothesis." However, several of these reports are speculative and rely on circumstantial evidence as to the exact cause of nestling mortality (Bent 1937, Ingram 1959, Crocoll and Parker 1989, Townsend 2006), a practice that is often inaccurate and unreliable (Pietz and Granfors 2000, Williams and Wood 2002). Understanding the effects of predator and non-predator causes of nestling mortality and nest failure on overall reproductive success is important in understanding the breeding ecology of any species and therefore, accurate identification of such causes is necessary.

Since 1997, we have studied a large population of Red-shouldered Hawks in suburban areas around Cincinnati, Ohio, by monitoring approximately 100 territories with active nests annually (Dykstra et al. 2000, 2009). Between 1998 and 2012, Red-shouldered Hawk nesting success (the percentage of nests that produce at least one fledgling) in the study area ranged from 51–67% (Dykstra et al. 2000, 2008, C. Dykstra unpubl. data), which is at the lower end of the range reported for other populations of this species (55–88%; Bednarz 1979, Armstrong and Euler 1982, Dijak et al. 1990, Jacobs and Jacobs 2002, Townsend 2006). However, reproductive rates of this suburban population were similar to those of a rural population in southeastern Ohio (1.7 ± 0.1 versus 1.6 ± 0.2 young/active nest/year, respectively; Dykstra et al. 2009). All of the causes of mortality and failure listed above are reported in other Red-shouldered Hawk populations, and are likely to occur in our suburban study area.

Without continuous observation of nesting activity, identification of the causes of nestling and adult mortality at the nest has been mostly speculative for

this and most other populations of Red-shouldered Hawks. Detailed studies of predator and non-predator causes of nest failure for Red-shouldered Hawks are lacking in the published literature, and there is no distinction between complete nest failure and individual nestling mortality in otherwise successful nests. Thus, our research objectives were (1) to identify predator and non-predator causes of nestling or adult mortality at the nest, and (2) to quantitatively distinguish between total nest success and individual nestling fate.

METHODS

Study Area. Our study area included parts of Hamilton, Clermont, and Warren counties near Cincinnati, Ohio, U.S.A. Suburban development varied from densely populated (residential lots approximately 20 m × 35 m) to sparsely populated (>2.5-ha residential lots and undeveloped private land; Dykstra et al. 2000). Nest trees were often located in private yards of residences and other buildings with nearby forested areas (Dykstra et al. 2003).

Locating and Monitoring Nests. In 2011 and 2012, we visited previously known Red-shouldered Hawk territories from mid-February until the end of March, prior to the emergence of leaves on deciduous trees. To locate nests, we searched historical nest areas from a vehicle and on foot, broadcast Red-shouldered Hawk territorial calls, and searched for stick nests if Red-shouldered Hawks responded or were seen (Dykstra et al. 2000, 2009). We also investigated nests reported to us by local residents.

Nests were considered occupied if there were signs of a nest being constructed or refurbished (e.g., hawk present, nest improved with green vegetation or fresh sticks; Dykstra et al. 2000). Nests were considered active if there was evidence that eggs had been laid, such as an incubating bird, broken eggshells at the base of the nest tree, small down feathers scattered around the edge of the nest, or excreta at the base of the nest tree (Dykstra et al. 2009). We monitored occupied and active nests from the ground using 10× binoculars or a 20–60× spotting scope. We selected potential camera nests based on the accessibility of the nest for climbers and written permission from the landowners.

Video Monitoring. Our digital video-monitoring systems (Townsend 2006, Benson et al. 2010, Cox et al. 2012) comprised a weatherproof 24-hr high resolution time-lapse color/infrared video camera and a mini digital video recorder (model AKR-200, Seorim Technology Co., Ltd., Seoul, South Korea;

product no. MDVR14-4, Supercircuits, Austin, Texas, U.S.A.), connected by a cable to a deep-cycle marine battery. The cameras were either an auto-focus camera (product no. PC177IRHR-8, Supercircuits, Austin, Texas, U.S.A.) mounted approximately 0.4–0.6 m above a nest or a far-range camera with variable-distance focus (product no. PC8017IR, Supercircuits, Austin, Texas, U.S.A.) mounted approximately 2 m from a nest. Prior to installation, we camouflaged the cameras with spray paint and bark to resemble each nest tree. We used an 18-cm handheld video monitor (model HLT 71, Haier, Camden, South Carolina, U.S.A.) to set the viewing angle and focus, and for checking the nest on subsequent visits.

Qualified tree-climbers installed cameras at selected nests either before eggs were laid (in occupied nests) or after eggs hatched. For the post-hatch camera nests in 2012, we determined the clutch size (n = two nests) or brood size (n = two nests) of active nests by using a mirror pole to view contents. At post-hatch nests in both years, we installed cameras when nestlings were estimated to be 4–10 d old, during mild to moderate weather conditions (e.g., no precipitation, wind, or intense sun exposure), with a minimum temperature of 15.5°C. The video/power cable was secured to the nest tree and strung to an adjacent tree approximately 8–15 m away. We placed a camouflaged plastic bin containing the MDVR and the battery at the base of this adjacent tree to reduce disturbance directly under the nest tree during subsequent visits. Video was recorded at a rate of 10 or 15 frames per second, with a 704 × 480 resolution. Ropel rodent repellent (Burlington Scientific, Farmingdale, New York, U.S.A.) was applied to the cables to discourage chewing by mammals. Cameras were removed after nest failure or after nestlings fledged.

In 2011 and 2012, we monitored 25 Red-shouldered Hawk nests with video cameras. In 2011, 11 nests received cameras: five prior to egg-laying, and six after eggs hatched. At the five nests that received a camera prior to egg-laying, all five Red-shouldered Hawk pairs laid eggs, indicating that mounting the cameras during the courtship phase, after the adults occupied the nest, did not cause abandonment. Therefore, we installed cameras prior to egg-laying at 10 Red-shouldered Hawk nests in the 2012 season (and again, all pairs laid eggs after camera installation). In addition to these 10 nests, four nests received cameras after eggs hatched, for a total of 14 nests monitored in 2012.

Measuring and Marking Nestlings. When installing cameras after nestlings hatched, the climber re-

moved the nestlings and lowered them to the ground for initial measurements and color-marking. This was also done during the first week after hatching for nestlings at those nests that received a camera prior to egg-laying. Nests with nestlings were only accessed during mild to moderate weather conditions as described above. We collected morphometric data including mass and wing chord, and if possible, tarsus length, seventh primary length, first and second secondary lengths, and toe-pad length, depending on the development of the nestlings.

To differentiate nestlings in video recordings, each nestling was marked with a nontoxic Sprayol™ liquid livestock dye (PBS Animal Health, Massillon, Ohio, U.S.A.; Townsend 2006). Dye colors (pink, orange, green, and blue) were assigned to individual nestlings in no particular order and dye was applied to the top of the nestlings' heads with a cloth or cotton balls. Nestlings were returned to the nest within approximately 30 min. Because nestlings were not large enough to hold leg bands until at least 2 wk of age, they were banded at 2–4 wk of age, but before the dye on their heads faded. Each nestling was then banded with a United States Geological Survey (U.S.G.S.) band on one leg and a unique, plastic, colored alphanumeric band (Haggie Engraving, Crumpton, Maryland, U.S.A.) on the other leg. During banding, we also re-dyed nestlings' heads and recorded morphometric data. We used the measurements of the first and second secondaries to determine hatch order and to estimate the age of nestlings at sites where cameras were mounted after eggs hatched (Penak et al. 2013).

Video Data Review. We visited each camera nest every 3 d to check its status and exchange the memory card and battery. During these nest checks, we used the video monitor to count the number of eggs or nestlings present. If we discovered that an egg or nestling was missing, or if the nest appeared otherwise disturbed at the time of the visit, we reviewed video to isolate the event in which the loss or disturbance occurred. We also reviewed overnight video footage to record the presence of a parent (usually the female; Miller 2013) each night during the incubation period. If a parent was not present overnight, we reviewed the video to search for a possible explanatory event at the nest.

RESULTS

Reproductive Success. Of the 25 nests monitored, eight (32.0%) failed completely, nine (36.0%) experienced some nestling mortality, and eight

(32.0%) fledged all nestlings, for an overall nest success of 68% (Fig. 1). By including the two nests where we obtained clutch size using a mirror pole, we monitored hatching success in 17 nests; a total of 55 eggs were laid (mean = 3.2 ± 0.56 eggs/clutch), and 13 eggs (23.6%) failed to hatch (Table 1). Two nests had partial hatching failure: at one nest, two of three eggs failed to hatch, and at another nest one of four eggs failed to hatch, which was likely caused by exposure to freezing overnight temperatures at the beginning of egg-laying (S. Miller unpubl. data). Three of these 17 nests (17.6%) failed completely during incubation: one due to the disappearance of the female parent, one due to depredation of the female parent by a Great Horned Owl, and one due to disturbance by an eastern grey squirrel (*Sciurus carolinensis*).

In the 22 camera nests that successfully hatched, at least one nestling, five (22.7%) failed completely, and 17 (77.3%) fledged at least one nestling (Fig. 1). Overall, 67 nestlings were hatched; 28 (41.8%) died before fledging, and 39 (58.2%) fledged successfully (Table 1, Fig. 2). Great Horned Owls were responsible for the deaths of 14 nestlings (20.8%) at five nests, and raccoons killed a total of four nestlings (5.9%) at two nests (Fig. 2). Non-predator causes of nestling mortality included starvation (four nestlings, 5.9%) and falls from the nest (five nestlings, 7.5%).

Mortality and Nest Failure. The primary cause of nestling mortality was depredation by Great Horned Owls, which occurred at five nests. In addition to depredation of nestlings, an owl killed the incubating female parent at a sixth nest, which was the only instance of an adult being killed in the nest. At four of the five nests with nestling depredation by owls, at least one parent hawk was present and survived the attacks. Raccoons, the only other predator documented by video monitoring in this study, killed four nestlings at two nests.

Two nests were disturbed by eastern gray squirrels; one had complete failure during the incubation stage, and one had a nestling mortality. In the first nest, incubation was repeatedly disrupted by a squirrel nesting in the bottom of the hawk's nest. The female hawk ultimately abandoned the nest after the squirrel flushed her and then ran across the nest, knocking out two of the three eggs. In the second nest, a squirrel ran at and struck the brooding female hawk in the breast, causing the hawk to jump up and tumble off the nest, ejecting one of the three nestlings.

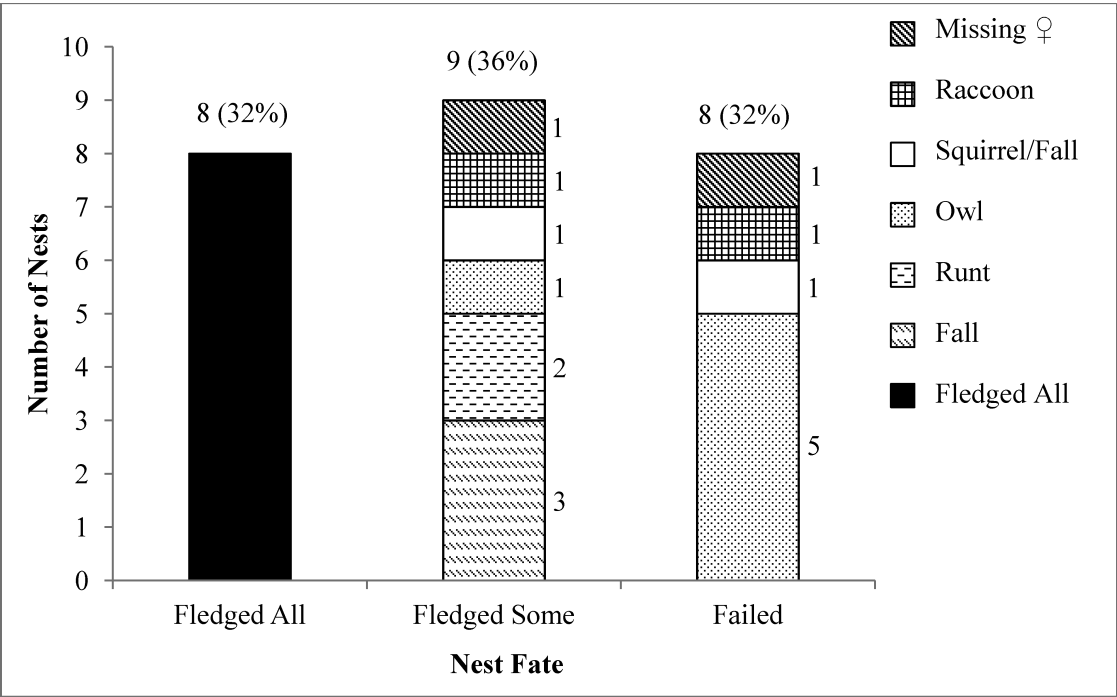


Figure 1. Fate of 25 Red-shouldered Hawk nests, including causes of nest failure or mortality in suburban eastern Cincinnati, Ohio, U.S.A. in 2011 and 2012.

Two nests had unexplained disappearances of parent females, one during incubation and one during the nestling period, which resulted in the starvation of the two youngest nestlings in a brood of three. These events were unrelated to camera installation, as they occurred 5 d and 32 d after installation, respectively, and behavior had been typical until that time (Miller 2013). Additionally, two last-hatched nestlings (runts) in two other nests were too small or weak to compete with older, larger

siblings and died within the first week after hatching, apparently of starvation.

Falling from the nest was the second-most common cause of nestling mortality, and was the fate of six nestlings (9.0% of 67 nestlings) at five nests: one fell over the edge as the female parent departed, one walked over the nest edge at night, one flopped over the edge seemingly due to lack of coordination from a physical ailment, one rolled off the edge at night while being brooded, one fell as part of the

Table 1. Differences between measures of reproductive success at video-monitored Red-shouldered Hawk nests in suburban Cincinnati, Ohio, U.S.A., in 2011 and 2012.

MEASURE OF SUCCESS	SAMPLING UNIT	NESTS (n)	SAMPLING UNIT (n)	SUCCESS %, (n)	FAILURE %, (n)
Hatching success	eggs	17	55	76.3%, (42)	23.6%, (13)
Fledging success	nestlings	25	67	58.2%, (39)	41.8%, (28)
Nest success ^a	nests	25	25	68.0%, (17)	32.0%, (8)
Nest success ^b	nests	15	15	60.0%, (9)	40.0%, (6)

^a All camera nests; 10 that received cameras post-hatch, and 15 that received cameras before egg-laying.
^b Only the 15 nests that received cameras before egg-laying, thereby capturing the entire nesting period. This measurement is most comparable to our typical measures of nest success (Dykstra et al. 2000, 2008, Miller 2013), in which we include only active nests (i.e., eggs laid) found before hatching.

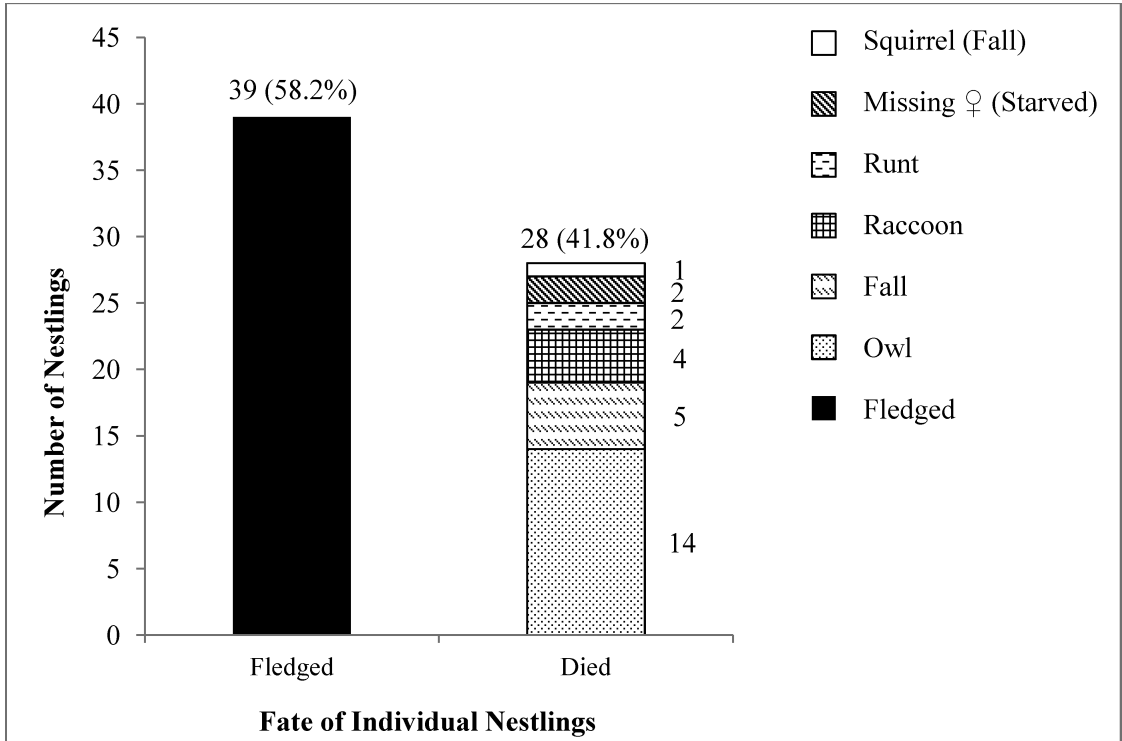


Figure 2. Fate of 67 nestlings, including causes of death, from 25 Red-shouldered Hawk nests in suburban eastern Cincinnati, Ohio, U.S.A. in 2011 and 2012.

nest became dislodged from the tree crotch, and one was ejected when the brooding female parent was attacked by a squirrel (as described previously).

DISCUSSION

At Red-shouldered Hawk nests monitored by video cameras in this suburban population, the primary cause of nest failure and adult or nestling mortality was depredation, mostly by Great Horned Owls. This study provides further evidence that Great Horned Owls are a common predator at raptor nests, and specifically at Red-shouldered Hawk nests, even in suburban environments. Falls from the nest comprised the second-most common cause of mortality of nestlings, and although the cause of each fall varied, none were the immediate result of sibling aggression or siblicide.

Interestingly, at two nests there were some losses caused by eastern gray squirrels. To our knowledge, this is the first documentation of eastern gray squirrels causing nest failure and nestling mortality, and is certainly the first case documented for the Red-shouldered Hawk. Other researchers (Bent 1937,

Stewart 1949, Campbell 1975) reported that Red-shouldered Hawks constructed nests on top of squirrel nests and attributed hawk nest abandonment or failure to the squirrels, but had no direct observations of conflicts. In our study area, it is fairly common for Red-shouldered Hawks to construct a nest on top of an old or current squirrel nest (C. Dykstra unpubl. data), so the potential for cohabitation and conflict exists within this population, and may be more prevalent than previously recognized. This interspecific conflict may be more significant for suburban-adapted raptors than for those nesting in more typical forested habitats due to the concurrent adaptation of squirrels to suburban environments, where a potentially limited number of suitable nest sites may lead to competition.

Four nestlings died due to apparent starvation; two of these were the last-hatched nestlings in their respective nests, and two were junior nestlings in a brood of three in a nest where the female parent disappeared. These deaths were consistent with Lack's (1947) hypothesis that asynchronous hatching and nestling size hierarchies are an adaptive

mechanism to facilitate brood reduction in times of food shortage. Because two of these nestlings perished before they could be color-marked, thereby prohibiting individual identification, we cannot definitively state that these deaths were due to food shortage or insufficient feeding rates by the parents. However, we note that at nests for which feeding rates were documented, the youngest (third-hatched) nestlings received significantly less food from the parents than the first-hatched nestlings (214.3 ± 53.0 g/nestling/30 hr of reviewed video vs. 253.3 ± 48.4 g/nestling/30 hr, respectively; $n = 16$ nests; 95% CI for the difference of means: $-69.9, -3.2$ g/nestling/30 hr; Miller 2013).

Although sibling aggression was intense at some nests in this population (Miller 2013), no nestling deaths were directly attributed to sibling aggression or siblicide, contrary to observations by Townsend (2006). However, we documented two incidents of cannibalism of dead nestlings by Red-shouldered Hawks in this study. In one case, the carcass of a fallen nestling was delivered by a parent and fed to its sibling; in another, parents ate the remains of their nestlings that had been killed by a raccoon. In contrast, in three nests that experienced brood reduction due to apparent starvation, carcasses were not cannibalized by the surviving siblings or parents. In Arkansas and Wisconsin, adult Red-shouldered Hawks also cannibalized nestlings, but the causes of the nestlings' deaths were not reported (Townsend 2006, Woodford et al. 2008). Thus, our study did not provide conclusive support of Alexander's (1974) "icebox hypothesis," that brood reduction occurs so that smaller offspring may serve as an extra food source for surviving siblings.

Video monitoring of Red-shouldered Hawk nests allowed continuous data collection and accurate identification of causes of mortality and failure at nests. Installing cameras prior to egg-laying conferred other advantages as well, including: minimization of disturbance that could lead to potential abandonment (compared to installation during incubation or early brood-rearing), the ability to record accurate times for egg-laying and hatching, and the documentation of incubation behavior and the earliest nestling behaviors. Without video monitoring, different conclusions may have been drawn about the fate of individual eggs or birds, or causes of nest failure. For example, a nestling found dead on the ground, but otherwise intact would have been a suspected victim of sibling aggression or a weather-related fall, but was actually pulled from the nest by a raccoon. Similarly, at two

nests with documented cannibalism, singular observations may have led researchers to assume the nestlings died from siblicide or infanticide, where in fact they died of other causes and were subsequently cannibalized. Additionally, when we found two broken eggs on the ground below a nest, we would have been inclined to suspect a Great Horned Owl depredating the parent, instead of the disturbance by a squirrel. Our study revealed that many causes of mortality could not be identified accurately without video monitoring, suggesting that researchers assessing causes of nest failure or mortality from the ground using a spotting scope should exercise caution and avoid speculation.

Distinguishing between overall nest success and individual hatching or fledging success provides a more complete description of reproductive success at Red-shouldered Hawk nests than a calculation of reproductive rate derived only from multiple visits to the nest. Simply reporting rates of nest success does not include quantification of hatching success or of total nestlings lost or fledged. Of the 25 camera nests (pre-laying and post-hatch) monitored, 68.0% ($n = 17$) fledged at least one nestling and 32.0% ($n = 8$) failed completely. This rate of nest success was comparable to those for the entire suburban population that we monitored using multiple nest visits; 57% ($n = 117$ active nests) and 67% ($n = 118$ active nests), in 2011 and 2012 respectively (Miller 2013), although success was measured in a slightly different way, as this camera study included eight nests that were entered into the dataset post-hatch, whereas our standard success rates (57% and 67%) included all active nests that were found prior to hatching. However, nine of the 17 successful nests experienced some nestling mortality, and the fledging success of individual nestlings was 58.2% (39 of 67 nestlings), as 28 nestlings (42.8%) died before fledging. As a caveat, we note that cameras were mounted post-hatch at eight nests for which clutch size was unknown, so it is possible that undocumented early loss of eggs or nestlings may have occurred before camera installation; therefore, the individual fledging success rate we report may be a slight overestimate. With more accurate identification of predator and non-predator causes of nestling mortality and nest failure throughout the nesting period, a more comprehensive account of reproductive success in this suburban population of Red-shouldered Hawks can be ascertained, which may provide insight into the subtleties of reproductive ecology for other species of raptors as well.

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