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Nest Defense Behavior of Suburban and Rural Red-shouldered Hawks†

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ABSTRACT.—Urban and suburban raptors live in close proximity to humans, and some species defend their nests and young vigorously, even diving at or striking humans walking on the ground. Such raptors may be more defensive of their nests than rural birds. We investigated (1) whether Red-shouldered Hawk (*Buteo lineatus*) nest defense behavior differs between suburban and rural birds, (2) whether any environmental conditions are associated with aggressive nest defense, and (3) whether nest defense behavior is associated with reproductive rate. First, we used an experimental walk-up protocol to approach nests with incubating or brooding Red-shouldered Hawks at suburban and rural sites, and we scored the hawk's response to our approach. We measured environmental variables (nest height, distance to the nearest road and nearest house, and habitat proportions within 500 m of the nest) and determined reproductive rate. Second, we used our historical database to retrospectively classify hawks as most aggressive, moderately aggressive, or not aggressive, and we measured the same environmental variables at their nest sites. We found that most birds at both suburban and rural study areas responded to our experimental approach with minimal nest defense, though suburban birds responded with higher levels of nest defense. Environmental variables were unrelated to nest defense intensity in the experimental study. For the retrospective study in the suburban area, nest height was the only environmental factor distinguishing aggressive hawks from non-aggressive ones; aggressive nest defensive behavior was associated with lower nests. Reproductive rate was unrelated to nest defense behavior in both studies. Knowing which environmental factors may contribute to more aggressive behavior may help researchers, managers, and residents better understand bird behavior and predict the circumstances under which problems might develop, particularly in urban/suburban environments.

KEY WORDS: *aggression*; *behavior*; *management*; *nest*; *nest defense*; *suburban*; *urban*; *wildlife conflict*.

COMPORTAMIENTO DE DEFENSA DEL NIDO DE *BUTEO LINEATUS* EN AMBIENTES SUBURBANOS Y RURALES

RESUMEN.—Las aves rapaces urbanas y suburbanas viven en estrecha proximidad a los humanos, habiendo especies que defienden vigorosamente sus nidos y crías, incluso lanzándose o golpeando a los seres humanos en el suelo. Estas rapaces podrían defender sus nidos aún mas que aquellas que habitan en áreas rurales. Investigamos (1) si el comportamiento de defensa del nido de *Buteo lineatus* difiere entre aves suburbanas y rurales, (2) si alguna condición ambiental está asociada con la defensa agresiva del nido, y (3) si el comportamiento de defensa del nido está asociado con la tasa reproductiva. En primer lugar, utilizamos un protocolo experimental de aproximación para acercarnos caminando a los nidos de *B. lineatus,* con ejemplares

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incubando o cuidando crías, tanto en sitios suburbanos como rurales, y puntuamos la respuesta a nuestro acercamiento. Medimos variables ambientales (altura del nido, distancia a la carretera más cercana y a la casa más cercana, y el porcentaje del tipo de hábitat dentro de un radio de 500 m del nido), y determinamos la tasa reproductiva. En segundo lugar, utilizamos nuestra base de datos histórica para clasificar retrospectivamente a los ejemplares de *B. lineatus* como muy agresivos, moderadamente agresivos o no agresivos, y medimos las mismas variables ambientales en sus lugares de nidificación. Encontramos que la mayoría de las aves en las áreas de estudio suburbanas y rurales respondieron a nuestro acercamiento experimental con una defensa mínima del nido, mientras que las aves suburbanas respondieron con los niveles más altos de defensa del nido. Las variables ambientales no estaban relacionadas con la intensidad de la defensa del nido en el estudio experimental. Para el estudio retrospectivo en el área suburbana, la altura del nido fue el único factor ambiental que distinguió a los ejemplares agresivos de los no agresivos; el comportamiento defensivo agresivo del nido se asoció con los nidos ubicados a menor altura. La tasa reproductiva no estuvo relacionada con el comportamiento de defensa del nido en ambos estudios. Identificar los factores ambientales que pueden contribuir a un comportamiento más agresivo puede ayudar a los investigadores, administradores y residentes a comprender mejor el comportamiento de estas aves y predecir dónde podrían presentarse este conflicto, particularmente en entornos urbanos/suburbanos.

[Traducción del equipo editorial]

INTRODUCTION

Raptors are increasingly inhabiting urban and suburban areas (Boal and Dykstra 2018, Kettel et al. 2018), where they frequently interact with humans. These interactions may be positive, as many urban human residents appreciate raptors as symbols of wilderness and enjoy watching their hunting and nesting behaviors (Arent et al. 2018). However, urban raptors also face a variety of challenges, including increased human disturbance, habitat fragmentation, and the presence of novel predators such as domestic cats (*Felis catus*) and humans (Dwyer et al. 2018) though predation is often reduced in urban areas (Tella et al. 1996, Lin et al. 2015). These factors may impact raptor nest defense behavior against humans (who may be perceived as predators or potential predators by the hawks); urban raptors sometimes display different nest defense behaviors than their rural counterparts. Some raptor species and individuals defend their nests and young vigorously, even diving at or striking humans on the ground, and this aggressive nest defense behavior can generate human-raptor conflict if birds nest near human developments (Davis 2018, Washburn 2018, Boal et al. 2022). Understanding whether certain environmental conditions make aggressive nest defense more likely can help researchers and managers predict the circumstances under which problems might develop, and may help affected residents better cope with defensive raptors.

Aggressive nest defense directed toward humans in urban areas has been reported for several species, including Mississippi Kites (*Ictinia mississippiensis*; Parker 1999, Skipper and Boal 2019, Boal et al. 2022), Black Kites (*Milvus migrans*; Kumar et al. 2019), Cooper's Hawks (*Accipiter cooperii*; Boal and Mannan 1999, Stout et al. 2006, Chiang et al. 2012), Barred Owls (*Strix varia*; Bierregaard 2018), and Red-shouldered Hawks (*Buteo lineatus*; Bloom and McCrary 1996). When nest defense behaviors of urban and rural birds are explicitly compared, urban raptors generally exhibit more aggressive nest defense against humans than their rural counterparts (Burrowing Owl [*Athene cunicularia*], Cavalli et al. 2016; Eurasian Sparrowhawk [*Accipiter nisus*], Kunca and Yosef 2016; Eurasian Goshawk [*Accipiter gentilis*], Merling de Chapa et al. 2020). However, the actual percentage of highly aggressive birds is low (Boal et al. 2022).

Environmental and nest-site characteristics may influence the intensity of raptors' nest defense behavior. A meta-analysis including mostly rural North American raptors that classified typical habitat broadly (i.e., open vs. closed land cover types) found that species that defend their nests more forcefully have more accessible nests (ground or tree nests vs. cliff or cavity nests) and perhaps inhabit more open cover types (grassland, desert, tundra; Morrison et al. 2006). This meta-analysis also suggested that nest defense against humans may be less aggressive than nest defense against avian predators, nocturnal or diurnal (Morrison et al. 2006). Higher levels of nest defense against humans are associated with low nest height (Andersen 1990), and greater human population in the surrounding area (Keeley and Bechard 2011) in some cases. Weather conditions (Fisher et al. 2004) and prey populations (Kontiainen et al. 2009) can also affect nest defense intensity.

Aggressive nest defense behavior confers an advantage if more aggressive birds experience positive outcomes such as greater reproductive success. For example, offspring recruitment numbers are most influenced by the nest defensiveness of female Ural Owls (*Strix uralensis*; Kontiainen et al. 2009), and Black Kites' nest defensiveness positively influences their reproductive success (Kumar et al. 2019). Theory predicts that the increasing investment parent raptors make as the breeding season progresses means nest defense should increase as the young age (the "offspring age" hypothesis; e.g., Wallin 1987, Redondo 1989, Tolonen and Korpimäki 1995) and that is supported in some studies (e.g., Galeotti et al. 2000, Fisher et al. 2004) but not others (Keeley and Bechard 2011, Møller and Nielsen 2014). For larger raptor species, the threat of predation may decrease as the young grow too large and capable of self-defense to be easily taken (the "offspring vulnerability" hypothesis), counteracting the theoretical increase in parental nest defense (Redondo 1989, Galeotti et al. 2000).

Red-shouldered Hawks, along with two accipiters and five species of falcons from North America, are classified as having very aggressive nest defense (in a meta-analysis that included accounts of defense against human and non-human potential predators; Morrison et al. 2006). A medium-sized buteo, the Red-shouldered Hawk inhabits forested or partly forested environments, particularly near riparian or wetland areas (Titus and Mosher 1981, Bednarz and Dinsmore 1982, Bosakowski et al. 1992, Dykstra et al. 2020) as well as urban areas (Bloom and McCrary 1996, Dykstra et al. 2000, 2020, 2021, Dykstra et al. 2023, Miller et al. 2023). Urban Red-shouldered Hawks nest and hunt in landscapes close to human disturbances including recreational activities (Bloom et al. 1993), and nest on average 75 m from the nearest home (Dykstra et al. 2000). Although most Red-shouldered Hawks do not strongly defend their nests against humans on the ground, some individuals dive at or strike people walking near their nests. Aggressive nest defense causing injuries to humans necessitates the capture and removal of some adults or the removal and fostering of aggressive pairs' broods (Bloom and McCrary 1996, Dykstra et al. 2018).

Our objectives in this study were to (1) determine whether nest defense behavior toward humans differs between suburban and rural birds, (2) assess whether any environmental conditions are associated with aggressive nest defense, and (3) evaluate whether the amount of nest defense behavior influences reproductive rate. Based on our field experience in the two study areas, we predicted that hawks would exhibit higher levels of nest defense at the suburban study area than at the rural study area. We also predicted that hawks would exhibit higher levels of nest defense at lower nests, nests closer to houses, and nests located in more-urban environments.

METHODS

Study Areas. We studied Red-shouldered Hawks in Hamilton, Clermont, Butler, and Warren Counties in suburban southwestern Ohio (SW Ohio hereafter), and in the Hocking Hills region of southeastern Ohio, in Hocking, Athens, Perry, and Vinton Counties (Supplemental Material Fig. S1). In SW Ohio, suburban development varied from densely populated (residential lots approximately 20 m $\times$ 35 m) to sparsely populated (>2.5-ha residential lots and undeveloped private land; Dykstra et al. 2000). For a related study in the same study area, we determined that buildings made up 5.7% $\pm$ 2.8% of the land-cover around nest sites (L. Dykstra unpubl. data). Native forests in the SW Ohio study area are primarily deciduous and are dominated by second-growth oak-hickory (*Quercus* spp. and *Carya* spp.) and beech-maple (*Fagus grandifolia* and *Acer saccharum*) associations, with lowland riparian forests characterized by sycamores (*Platanus occidentalis*) and beech. Red-shouldered Hawk nests were located primarily on private land, in yards of residences or in nearby forested areas.

The Hocking Hills study area, approximately 180 km east of the SW Ohio study area, is heavily forested with a sparse human population. We found nests in Wayne National Forest, Hocking State Forest, Zaleski State Forest, and associated private lands. The predominant forest type is deciduous (oak-hickory), but plantations of white pine (*Pinus strobus*) and red pine (*P. resinosa*) are also common. Lowland forests are characterized by sycamores, silver maple (*Acer saccharinum*), beech, and river birch (*Betula nigra*). Proximity of nests to human activities varied widely, with some areas containing residential development, some recreational development such as hiking trails and picnic areas, and some fairly remote (Dykstra et al. 2000). Buildings made up only 0.3% $\pm$ 0.4% of the land-cover of this region (L. Dykstra unpubl. data).

We use the term suburban to describe our SW Ohio study area to maintain consistency with our prior work (Dykstra et al. 2000, 2009, 2021, Dykstra et al. 2023, Miller et al. 2023) and because it seems to better describe most of our nest sites in SW

Ohio. However, we acknowledge that the terms urban, suburban, exurban, and rural have been undefined or used with varying definitions in the literature (Dykstra 2018). For discussion of others' research, we simply use the term urban for all landcover types within cities and suburbs and the term rural for more natural areas with low human population (as in Dykstra 2018).

Nests and Productivity. As part of our long-term study of Red-shouldered Hawk reproductive rate (Dykstra et al. 2000, 2009, 2021), we routinely searched for nests in all known nesting territories (defined as in Steenhof and Newton 2007) between mid-February and mid-April. We included nests in our productivity database if there was evidence that eggs had been laid (i.e., incubating adult, presence of small down feathers on the edges of nest, or broken eggshells below nest; also called "active nest"). A nest with eggs in a year was considered a nesting attempt (Steenhof and Newton 2007). All nesting attempts were found during the courtship or incubation phases.

We accessed many nests using approved climbing techniques when the nestlings were 2–5 wk old (May–June) to count and band the nestlings. Climbers wore helmets, and typically attempted to redirect incoming aggressive hawks by making eye contact, waving, and shouting. We counted nestlings as "fledged" if they were at least 3 wk old (as in Dykstra et al. 2021), based on the mean length of the first and second secondary (Penak et al. 2013). If a nest was inaccessible, permission to climb could not be obtained, or the nestlings were <3 wk at banding, we used a spotting scope to count the young when they were 4–6 wk old.

Experimental Nest Defense Study in Suburban and Rural Study Areas. In 2015–2016, we measured nest defense behavior at nests in both the suburban and rural study areas (Supplemental Material Fig. S1). We considered all 2015 nesting attempts as candidates for inclusion in the experimental study, and we selected nests based on permissions from landowners and scheduling logistics. In 2016, we did not retest the birds at any nesting territory we had studied in 2015. We conducted trials between 0800 H and 1830 H, 17 March–26 May, 2015 and 2016, and we did not conduct trials in the rain.

We used an experimental "walk-up" protocol similar to that used in prior studies (Cavalli et al. 2016, Boal et al. 2022). At the start of each trial, the researcher parked the vehicle at least 100 m from the nest and determined if a hawk was present at the nest. If a hawk was present on the nest, the researcher recorded the air temperature, sky conditions, number of people present, and the time. The researcher began the trial at 50–60 m from the nest by starting a timer and then walked slowly to the nest in as straight an approach as possible, watching the hawk constantly. After reaching the nest, the researcher slowly returned to the start point while still watching the hawk by turning back to look at the nest occasionally. At the starting point, the researcher checked the timer; if <2 min had elapsed, the researcher continued watching the hawk until the full 2 min had elapsed. In some locations where thick vegetation precluded easy viewing, a second researcher with a spotting scope watched the hawk from a distance while the first walked to the nest and back. Based on a modification of Morrison et al. (2006), we listed seven ordinal categories of hawk response, and the researcher chose the one which best described hawk behavior: (1) hawk flushed from nest and flew away; (2) hawk remained in the nest, either showing no detectable response or looking at the researcher but not moving or vocalizing; (3) hawk initiated or increased vocalizations but remained in the same position; (4) hawk stood up and moved around in the nest; may also have initiated or increased vocalizations; (5) hawk moved between branches or nearby trees; may also have initiated or increased vocalizations; (6) hawk flew at researcher but did not make contact; (7) hawk flew at and hit researcher. If a second hawk was nearby or responded, we also made notes on its behavior. As in other studies (Galeotti et al. 2000, Sergio and Bogliani 2001, Kunca and Yosef 2016, Arroyo et al. 2017, Traisnel and Pichegru 2017 [non-raptor]), we considered a bird remaining on its nest to be exhibiting a greater level of nest defense than one flushing and flying away from the approaching researcher; remaining in the nest has been termed the "alert" response (Kunca and Yosef 2016) or "passive presence" (Arroyo et al. 2017) in other studies. This classification agreed with our previous observations of Red-shouldered Hawk behavior over 20 yr of field studies in which we found that individuals that fled from the nest did so quietly (C. Dykstra unpubl. data) in the direction away from the approaching researcher, suggesting avoidance or fear.

We attempted to conduct a trial at two phases of the breeding period (incubation and the nestling-rearing phase [when young were approximately 0–2 wk old]) at each nest. In some cases (n = 27 SW Ohio and n = 18 Hocking Hills), we were unable to conduct both trials, generally because the nest failed between the first trial and the

nestling-rearing phase; these nests were excluded from our analyses. We defined productivity for the sampled nests in this study as the number of fledged young per nest where the eggs hatched and nestlings survived to the nestling-rearing stage.

After the breeding season, we assessed environmental variables in the area immediately surrounding the studied nests. We selected environmental variables that might be expected to influence nest defense behavior, based on our field experience and the literature (Andersen 1990, Keeley and Bechard 2011). We measured the height of the nest above ground (m), the distance from the nest tree to the nearest human residence (house or apartment building [excluding outbuildings such as sheds]; m), and the distance from the nest tree to the nearest road (m); we used a tape measure for short distances, a rangefinder for longer distances, and a clinometer for nest height.

We created a circular plot of radius 500 m around each nest and calculated the proportion of land cover types (National Land Cover Database [2016]; https://www.mrlc.gov/data) within these plots using ArcGIS version 9.1 (as in Dykstra et al. 2021). Land cover types included deciduous forest, coniferous forest, mixed forest, pasture/hay, cultivated crops, developed high-intensity residential, developed medium-intensity residential, developed low-intensity residential, and developed open space. Several land cover types made up a small proportion of the plots, so we pooled deciduous forest with mixed forest (hereafter, deciduous forest), pasture/hay with cultivated crops (hereafter, pasture/crops), and developed medium-intensity residential with developed low-intensity residential (hereafter, low–medium intensity residential) land covers. Rather than include all possible land-cover types, we sought one or a few variables that described the suburban nature of the nesting sites. The proportion of the main suburban land cover type (low–medium intensity residential) and the proportion of deciduous forest within the plots were inversely correlated (Pearson's $r = -0.91$; Fig. S2), and we judged deciduous forest as more suitable for analyses because the proportion of residential land cover was close to 0 at some Hocking Hills sites (Table S1.) We considered the proportion of deciduous forest land cover to be an index to the amount of suburban development, as these two cover types made up the majority of land cover in our study areas and were highly (inversely) correlated.

Retrospective Study of Nest Defense Behavior in the Suburban Study Area. To increase the sample size of nesting territories where birds defended their nests aggressively and to gain further insight into environmental factors associated with nest defense, we used our long-term database—which included notes on defensive behavior recorded during nest visits and comments from landowners—to conduct a retrospective analysis. Using our most recent 5 yr of data (our 2011–2015 data set, which incidentally included 13 nests from the experimental study), we classified three levels of hawk nest-defense behavior at active nests within our suburban study area: (1) Unaggressive—the hawks had never been known to hit or dive at anyone; (2) Moderately aggressive—a hawk either hit or dove at a climber in the nest tree; (3) Most aggressive—a hawk either hit or dove at a resident or researcher on the ground near the nest. We considered that walking on the ground was less provocative than climbing to the nest, so hawk aggression against people on the ground was classified as the highest level of nest defense. Because of the retrospective nature of the study, not all nesting territories in our study area could be classified with confidence, which potentially may have introduced some bias into the dataset. For the moderately aggressive birds (category 2), our records provided a complete tally of all nesting territories where a climber was hit or a bird dove aggressively at the climber. For the most aggressive birds (category 3), we included nesting territories where a hawk hit or dove at a researcher on the ground and those where a landowner or neighbor reported such aggression to us. This is likely an incomplete tally of all such nesting territories in our study area, because landowners may not have reported aggression to us. For the unaggressive birds (category 1), we reviewed our historical database looking for nesting territories without a record of aggressive nest defense behavior, and then we interviewed the resident landowners and asked specifically if the hawks had ever hit or dove at anyone. If the landowners confirmed there had been no aggression (to their knowledge), we included that nesting territory in category 1. If the landowner reported any aggressive nest defense behavior by a hawk, we included that nesting territory in category 3.

For hawks with multiple years of data in 2011–2015, we included only the most recent year of data in our dataset for analysis, to avoid pseudo-replication. If hawks in a nesting territory could be categorized as both most aggressive and moderately aggressive (i.e., hit or dove at both climbers and people on the ground; $n = 5$), we classified them as most

aggressive. Interviews of landowners in 2016 identified one additional 2016 nesting territory in category 3, and four 2016 nesting territories in category 1, so these were also added to the dataset.

We considered all 2011–2015 nesting attempts in our study area candidates for inclusion in the retrospective study; however, because category 2 necessarily contained only nests where we climbed to band nestlings, no nesting attempts where eggs failed to hatch could be included. Thus, to make the productivity calculation for the three categories comparable, we limited the dataset for all three categories to only nesting attempts where the eggs hatched. Therefore, we defined productivity for the sampled nests as the number of fledged young per nest where eggs hatched.

After the breeding season, we measured the height of the nest, distance from the nest to the nearest residence and nearest road, and we assessed environmental variables as above (Table S2). As for the experimental study, the proportions of the primary suburban land cover type (low–medium intensity residential) and of deciduous forest were highly correlated ($r = -0.84$), and we selected the proportion of deciduous forest as an index to the amount of suburban development, as above. We similarly predicted that hawks would exhibit higher levels of nest defense at lower nests, nests closer to houses, and nests located in more urban/less-forested environments.

Statistical Analyses. *Experimental nest defense study in two study areas.* Red-shouldered Hawk responses in our trial were less intense than those classified in Morrison et al. (2006); because there were very few hawk responses classified as levels 3–5 and none classified as 6–7, we pooled all responses classified as level 3–5 as 3+. We used Fisher Exact tests to determine whether the distribution of survey responses (1, 2, or 3+) differed between Hocking Hills and SW Ohio, during the incubation and nestling-rearing phases separately. Within each site, we also used Fisher Exact tests to determine whether the distribution of survey responses changed between the incubation phase and the nestling-rearing phase.

We standardized the environmental variables (nest height, distance to house, distance to road, and proportion of forest) with a mean of 0 and SD of 1 for all analyses. Because there was a low number of 3+ responses, we simply used univariate Kruskal-Wallis tests to determine whether the standardized variables differed among the three response groups (responses 1, 2, and 3+). We tested Hocking Hills and SW Ohio separately, so that differences inherent in the two sites would not overwhelm differences among the response groups. *P*-values were Bonferroni-adjusted to account for multiple tests ($n = 16$ tests).

We used Kruskal-Wallis tests to assess whether productivity (i.e., the number of young produced; range = 0–4) differed among hawks with different nest defense behaviors (response 1, 2, or 3+). Study areas were combined for this analysis, but we also tested study areas separately and found similar results.

Retrospective study in the suburban study area. We standardized the environmental variables (nest height, distance to house, distance to road, and proportion of forest) with a mean of 0 and SD of 1 for all analyses. We modeled the influence of the environmental factors on nest defense behavior by using ordinal logistic regression (ordinal response variable: unaggressive, moderately aggressive, most aggressive; link function: logit) using the function *polr* in the R package *MASS* (Ripley et al. 2013). Predictor variables were tested for collinearity prior to inclusion in the model. We used a backward stepwise procedure, starting with all four explanatory variables, then deleting the least significant, until only significant variables remained. We report results using the standardized coefficients.

We used Kruskal-Wallis tests to assess whether nest defense behavior in three categories (most aggressive, moderately aggressive, or unaggressive) was related to productivity. Analyses were conducted in R version 4.3.2 (R Core Team 2023).

RESULTS

Experimental Nest Defense Study in Suburban and Rural Study Areas. We conducted trials at 64 nests during both incubation and the nestling-rearing phase ($n = 42$ SW Ohio and $n = 22$ Hocking Hills). Most birds at both sites responded to our experimental approach by staying on their nest (response 2; Fig. 1); these birds generally appeared to be aware of the approaching person and often watched the researcher walk toward the nest, but maintained their position in the nest despite the intrusion. Few birds at either site responded vigorously, so we pooled responses 3–5 as 3+ for all further analyses. The distribution of hawk responses (1, 2, or 3+) differed between Hocking Hills and SW Ohio, during both the incubation phase (Fisher Exact test, $P = 0.005$) and the nestling-rearing phase ($P = 0.001$). Comparatively more Hocking Hills birds responded to our experimental approach by flushing and flying away (i.e., the lowest level of nest defense). Comparatively more SW Ohio birds responded by

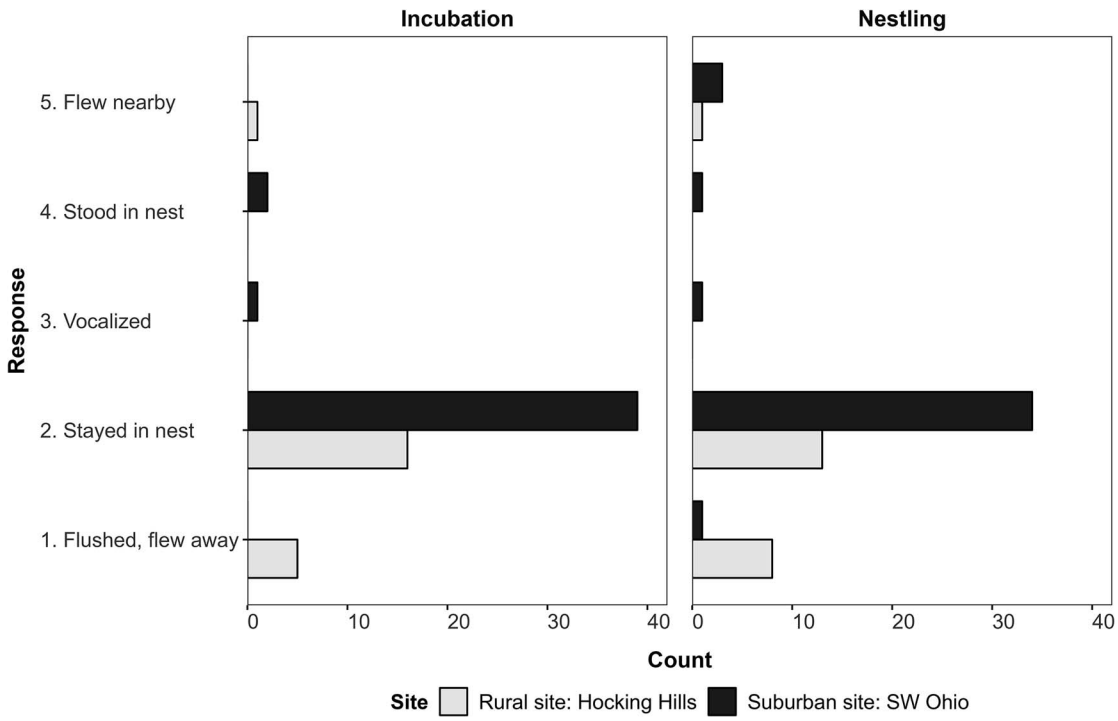

Figure 1. Red-shouldered Hawk responses to an experimental test of nest defense behavior, during the incubation and nestling-rearing phases, at suburban and rural study areas in southern Ohio. Responses are ordered from least aggressive (response 1) to most aggressive (response 5) following a modification of Morrison et al. (2006). Distributions of responses differed significantly for both phases.

staying on their nests (Fig. 1), which we interpreted as a higher level of nest defense.

The distribution of hawks' responses to the surveys did not differ between the incubation phase and the nestling-rearing phase, at either the Hocking Hills (Fisher Exact test, $P = 0.747$) or the SW Ohio ($P = 0.481$) study area.

Within each site, none of the environmental variables differed among response groups (responses 1, 2, and 3+), either for the incubation or for the nestling-rearing periods (Kruskal-Wallis; all $P > 0.05/16$; Fig. 2). The number of young produced per nest was unrelated to the level of nest defense behavior during incubation (Kruskal-Wallis; $P = 0.911$) and during the nestling-rearing phase ($P = 0.479$; Fig. S3).

Retrospective Study of Nest Defense Behavior in the Suburban Study Area. Red-shouldered Hawks at 203 SW Ohio nesting territories made at least one nesting attempt each in 2011–2015. Of these, 21 birds or pairs of birds (10.3% of the 203 territories) displayed highly aggressive nest defense (category 3) at least once during this time and 25 (12.3%) exhibited moderately aggressive nest defense (category 2) at least once, for a total of 46 (22.7%). For comparison, we studied 25 nesting territories where hawks were not aggressive, to our knowledge (category 1). One 2016 nest was added to category 3, for a total sample size of 72.

Ordinal logistic regression modeling indicated that only nest height significantly influenced the level of aggression of parental nest defense (Fig. 3). The probability of aggression decreased with increasing nest height ($\beta = -1.038 \pm 0.271$, $Z = -3.83$, $P < 0.001$).

As in the experimental study, the number of young produced per nest was unrelated to the level of nest defense behavior (Kruskal-Wallis; $P = 0.1914$).

DISCUSSION

Suburban Red-shouldered Hawks displayed more intense nest defense toward humans than their rural counterparts in our experimental study, though

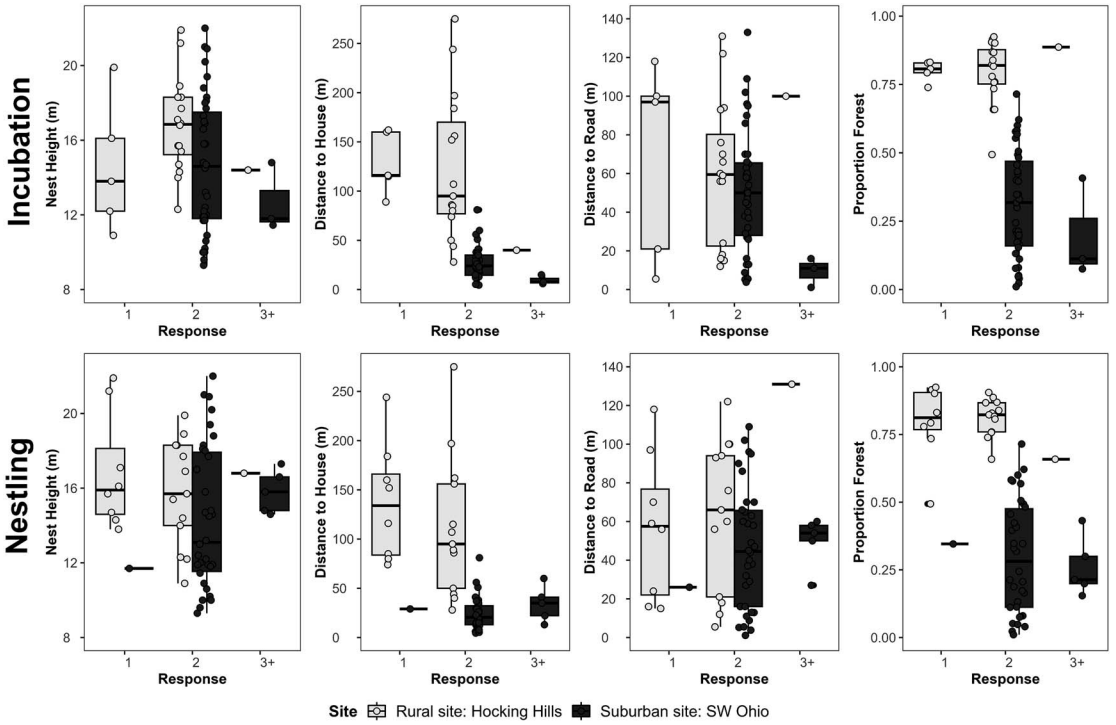

Figure 2. Environmental variables did not differ among Red-shouldered Hawk nests where birds exhibited different levels of nest defense behavior in response to an experimental test. Tests conducted at suburban and rural study areas in southern Ohio during incubation and the nestling-rearing phases. Ordered responses: response 1= flushed and flew away; response 2 = stayed on nest; response 3+ = vocalized, stood up in nest, or flew nearby. Note that there were no suburban hawks that displayed response 1 during incubation, so only rural hawks are shown for that response.

most hawks simply remained on their nest when a researcher approached. Although the low variability of responses in that study precluded analysis of the influence of environmental variables, our retrospective study in the suburban study area indicated that lower nests were linked to more aggressive nest defense. However, the level of nest defense was unrelated to a pair's productivity in both studies. Thus, some of our predictions were supported; however, we were unable to detect an advantage for aggressive nest defense in terms of reproductive rate.

Nest Defense in Urban vs. Rural Habitats. Suburban Red-shouldered Hawks almost never flushed from the nest and flew away as we approached, but a significant proportion of hawks in our rural Hocking Hills study area did. This aligned well with our previous observations during nest surveys in the two study areas (C. Dykstra and J. Hays unpubl. data), and suggests that rural birds are less willing to stay and defend their eggs or young, and thus exhibit lower levels of nest defense behavior. In addition, Red-shouldered Hawk responses to our climbing to nests also support this interpretation: in rural Hocking Hills, the researcher (CRD or JLH) was struck by a hawk on 8 of 226 (3.5%) climbs to nests when nestlings were present (1997–2016; 108 nesting territories total), compared to 10.8% of climbs to nests in suburban SW Ohio (18 of 166 climbs, 2011–2015; $Z = -2.70$, $P = 0.007$; C. Dykstra and J. Hays unpubl. data).

Urban raptors typically defend their nests against humans more vigorously than do conspecifics in rural habitats (Cavalli et al. 2016, Kunca and Yosef 2016, Merling de Chapa et al. 2020). Nesting Burrowing Owls may raise their feathers, hover over the intruder, or dive at them, and they exhibit higher levels of defense in urban areas and toward a person with a dog than toward a person alone (Cavalli et al. 2016). Eurasian Sparrowhawks make warning calls or beat their wings against the nest (Kunca and Yosef 2016), with the more aggressive responses more common at urban nest sites. In

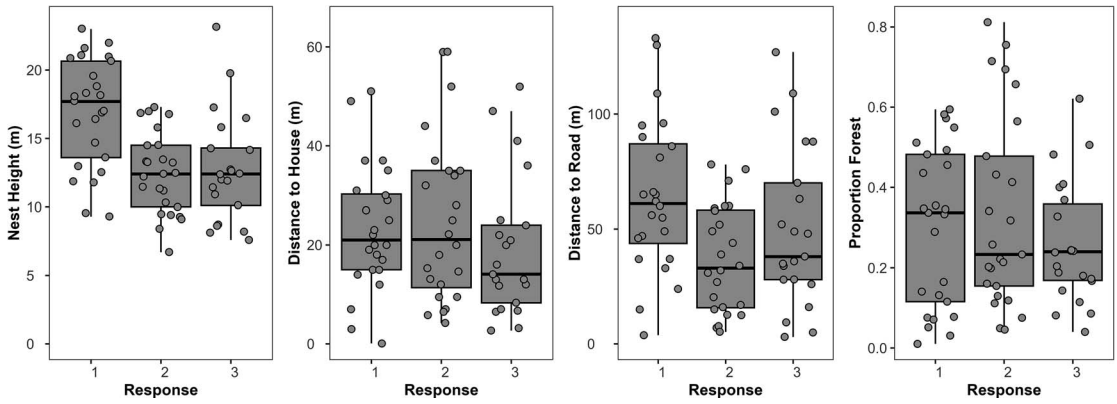

Figure 3. Nest height was the most important environmental variable associated with levels of nest defense behavior of suburban Red-shouldered Hawks in our retrospective study. Categories of hawks' nest-defensiveness: 1 = unaggressive (not known to hit or dive at anyone); 2 = moderately aggressive (hit or dove at a researcher in the nest tree); 3 = most aggressive (hit or dove at a person on the ground).

Germany, urban Eurasian Goshawks alarm-call and make passes at a climber at much higher rates than do their conspecifics nesting in nearby rural landscapes (Merling de Chapa et al. 2020). Mississippi Kites' responses to researchers' experimental approaches also differed between rural and urban areas: although approximately the same percentage of birds responded by diving at the researcher at the two sites (21% and 16%, for rural and urban respectively), more rural birds than urban birds responded by flushing and flying away (15% vs. 0%, respectively) and most stayed in the nest (59% vs. 84%, respectively), as in our study (Skipper and Boal 2019). In addition, rural kites flushed at a greater distance than urban ones (Skipper and Boal 2019). However, Skipper and Boal (2019) classified staying in the nest as response 0 ("no response"), a less-intense response than flushing and flying away, which was classified as response 1 ("flight response"). Conversely, other researchers (Galeotti et al. 2000, Sergio and Bogliani 2001, Kunca and Yosef 2016, Arroyo et al. 2017) classified staying in the nest as a more intense defense behavior than flying away, as in our study. In our experience, Red-shouldered Hawks that flushed slipped away quietly before the researcher arrived at the nest, flew in the direction away from the researcher, and remained silent, generally hidden in the forest (C. Dykstra, J. Hays, and M. Simon unpubl. data); this behavior suggested fear or avoidance (and perhaps also served to hide the location of the nest from an approaching predator). Red-shouldered Hawks that remained in the nest generally appeared to be aware of the researcher and often watched the researcher walk toward the nest, but maintained their position in the nest despite the intrusion. Although a bird that remains in its nest may appear simply indifferent to the human disturbance, we consider that such a bird is bolder than the one that flushes and flies off into the forest. We are confident that our ordered response scale was appropriate for Red-shouldered Hawks, but we acknowledge there may be differences among species.

Proposed explanations for more aggressive nest defense by urban raptors against humans often invoke the amount of time or number of interactions raptors have had with humans, and the outcome of those interactions (Andersen 1990, Morrison et al. 2006, Kumar et al. 2018). Raptors that experience frequent interactions with humans with few negative outcomes (i.e., low threat) may feel free to defend their nests vigorously (Morrison et al. 2006). In many modern cities and suburbs, raptors see humans often but rarely experience persecution from them, so the perceived threat is likely low. As an example, nest defense by urban Black Kites in Delhi, India, is greater in urban sites, particularly in areas with dense Muslim populations (where kites are hand-fed as part of religious practices) and areas with poor sanitation (Kumar et al. 2018). Repeated nonlethal interactions/disturbances by humans can habituate raptors (Ferrer et al. 2007, Arroyo et al. 2017, Kumar et al. 2019, Merling de Chapa et al. 2020, Morozov 2022) and thus one consequence of increasing protection for raptors may be some increase in aggressive nest defense (Ferrer et al. 2007, Arroyo et al. 2017, Kumar et al. 2019). The converse is also true:

raptors and corvids in areas with more persecution defend their nests less intensely (Knight et al. 1987, Galeotti et al. 2000, Wright et al. 2019).

The rapid development of behavioral differences between neighboring urban and rural populations may be attributable to the behavioral flexibility of urban species, or to the influences of microevolutionary processes (Carrete and Tella 2011, Rebolo-Ifrán et al. 2015, Arroyo et al. 2017, Kumar et al. 2019). The selection pressure of human disturbance/urban development may favor tame or tolerant individuals of species that have a wide variability in behavior (Carrete and Tella 2011); shyer, less-tolerant individuals may be relegated to areas farther from human disturbance, such as rural regions.

Influence of Environmental Variables on Nest Defense Behavior. Our retrospective study in suburban SW Ohio indicated that nest height influenced the aggressiveness of nest defense behavior against humans. Red-shouldered Hawks with more aggressive nest defense had nests averaging 4.6 m lower than those of unaggressive birds. Similarly, Red-tailed Hawks' (*Buteo jamaicensis*) calling defense behavior was inversely related to nest height (Andersen 1990). In contrast, nest defense intensity toward human researchers was unrelated to nest height among rural and exurban Ferruginous Hawks (*Buteo regalis*; Keeley and Bechard 2011) and Mississippi Kites (Skipper and Boal 2019). Among North American diurnal raptors, species with more accessible nests also exhibit more intense nest defense behavior (Morrison et al. 2006), so it is possible that the same relationship might prevail within a species as well. Lower nests would be more accessible to potential terrestrial predators such as raccoons (*Procyon lotor*), important predators of Red-shouldered Hawks in Cincinnati (Miller et al. 2015), and humans. In addition, these potential predators, even when on the ground, would be physically nearer to an adult hawk in a low nest, and that proximity might provoke the hawk to defend aggressively.

The limited variability of responses in our experimental study precluded a robust analysis of the influence of environmental variables on hawk responses, and we found no differences in the means of the environmental variables among response groups. It seems apparent that the 2-min walking test we performed was not sufficiently provocative to elicit strong defense responses. A more severe threat, such as a climber ascending the nest tree, likely would have engendered a more aggressive nest defense and/or a wider range of response behaviors (Andersen 1990, Kontiainen et al. 2009, Møller and Nielsen 2014). Other similar studies in which the researchers walked to the nest but then remained standing at the nest for 10 min (Keeley and Bechard 2011) or 5 min (Andersen 1990) provoked more intense defense by Ferruginous Hawks and Red-tailed Hawks, respectively. The methodology differences between those studies, the current study, and the Mississippi Kite studies (Skipper and Boal 2019, Boal et al. 2022) may explain the more limited responses in the last two (Skipper and Boal 2019).

Our retrospective approach circumvented the issue of limited responses by identifying sites with hawks that exhibited different levels of nest defense and then characterizing nest sites. This approach allowed multivariate modeling to assess the significance of environmental variables, but we acknowledge that the study design may have inadvertently introduced some bias into the dataset, because not all nesting sites could be classified and nests entered the study in different ways. In addition, the retrospective study did not allow us to assess nest defense at different phases of the nesting period, or at the rural study area, where nests are typically far from human developments (Dykstra et al. 2000). However, we feel our retrospective approach captured the extent of aggressive nest defense within the suburban study area better than the single experimental trial, because even the most defensive Red-shouldered Hawks do not respond aggressively every time a person approaches the nest. In particular, nest defense intensity typically decreases when more people are present (Mo and Waterhouse 2021, C. Dykstra and J. Hays unpubl. data). The retrospective approach integrated nest defense behavior over a period as long as 5 yr because we classified hawk behavior as aggressive if the birds exhibited that behavior any time during the 5-yr period (though we included only one data-year for each pair to ensure data independence).

Factors other than environmental variables that likely influence raptor nest defense behavior include bird age and experience (Møller and Nielsen 2014) and the individual birds' personalities. Animal personality traits are repeatable and stable (Réale et al. 2007, Bell et al. 2009), and one commonly described personality trait is boldness (i.e., the boldness-shyness continuum; Carere and van Oers 2004, Brommer et al. 2014). Nest defense behavior of raptors is generally repeatable among Ural Owls (Kontiainen et al. 2009), Tawny Owls (*Strix aluco*; Brommer et al. 2014), and Montagu's Harriers (*Circus pygargus*; Arroyo et al. 2017), indicating that nest defensive behavior may reflect an individual bird's personality. Personality is at least

partly heritable (Réale et al. 2007), which suggests that raptor nest defense behavior may be influenced by intrinsic qualities of the individual as well as by environmental variables such as nest height and habitat. Our anecdotal evidence supports this interpretation, as aggressive Red-shouldered Hawks in our study areas behaved similarly year after year (J. Hays and C. Dykstra unpubl. data).

Reproductive Rate. Red-shouldered Hawk nest defense behavior was unrelated to productivity in both of our studies. This was not unexpected, because our study design excluded nests that failed during the incubation phase, which limited our sample to only the more successful birds, reducing variability. Similarly, a comprehensive study of nest defense detected no relationship between nest defense levels and measures of reproductive output in Eurasian Goshawks (Møller and Nielsen 2014). In contrast, nest defensive behavior of Ural Owls (Kontiainen et al. 2009) and Black Kites (Kumar et al. 2019) was positively associated with some measure of reproductive rate. Black Kites increased their defense as the nesting season progressed, and nest defense intensity was also positively related to the number of young produced (Kumar et al. 2018), though the mechanism of this relationship was unclear. One possible explanation for an association between defensive behavior and reproductive success is that higher-quality parents are both more defensive and produce more young (Kumar et al. 2018). Brommer et al. (2014) found that an apparent association between nest defense behavior and reproductive success of Tawny Owls was actually better explained by the covariance of boldness with early breeding. Although theory suggests that better nest defense behavior should result in greater reproductive success (e.g., Kontiainen 2009), many other factors affect reproductive rate including food and weather (Newton 1979). In our study areas, warmer May temperatures and increasing amounts of coniferous forest cover were associated with greater Red-shouldered Hawk reproductive rates (Dykstra et al. 2021).

Conservation Implications. Nest defense behavior of urban raptors can create wildlife-human conflict if the humans are severely injured by the birds or if they perceive that they might be (Davis 2018, Washburn 2018). Actual percentages of highly aggressive birds are low (Bijlsma 2008, Boal et al. 2022, this study), though media attention tends to distort public perception (Boal et al. 2022). Knowing which environmental factors contribute to more aggressive behavior may help researchers, managers, and residents better understand bird behavior. Providing effective advice to reduce injury (i.e., avoid the nest area, wear a hard hat, carry an umbrella; Bijlsma 2008, Dykstra et al. 2018) can also help alleviate fears and increase local compliance. In our study area (Dykstra 2018) and elsewhere (Davis 2018, Pagel et al. 2018, Kumar et al. 2019), most residents appreciate local raptors, enjoy having them nesting nearby, and tolerate their occasional nest defensive behaviors even if they cause injury. As urbanization continues to increase, escalating interactions with wildlife may be expected, and the importance of involving urban residents in conservation discussions and decisions about raptors can only increase as well (Davis 2018, Kumar et al. 2019).

SUPPLEMENTAL MATERIAL (available online). Figure S1: (a) Study areas in suburban SW Ohio and rural Hocking Hills for experimental study; (b) Nest sites in SW Ohio, for retrospective study. Figure S2: Correlation of the proportion of low-and-medium-intensity residential development and the proportion of deciduous forest within 500-m-radius plots centered on nest sites for the experimental study of Red-shouldered Hawk nest defense behavior. Figure S3: Productivity (number of young fledged per nest) did not differ among Red-shouldered Hawk nests where birds exhibited different levels of nest defense behavior in response to the experimental test. Table S1: Proportion of land cover types in 500-m-radius circular plots centered on nests of Red-shouldered Hawks for the experimental study of nest defense behavior. Table S2: Proportion of land cover types in 500-m-radius circular plots centered on nests of Red-shouldered Hawks for the retrospective study of nest defense behavior.

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