SHORT COMMUNICATIONS

SPATIAL AND TEMPORAL VARIATION IN REPRODUCTIVE RATES OF THE RED-SHOULDERED HAWK IN SUBURBAN AND RURAL OHIO

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Abstract. We measured the reproductive rate of Red-shouldered Hawks (*Buteo lineatus*) nesting in suburban southwestern Ohio and in a rural forested region in Hocking Hills, southeastern Ohio, from 1997 to 2005. In the suburban region, the reproductive rate varied greatly from nest to nest, less so from year to year, indicating that some nest areas consistently produced more young than others. The most productive 25% of nest areas produced 44% of all the nestlings in the study, whereas the least productive 25% of nest areas produced only 7% of all nestlings. In the rural area, the reproductive rate varied significantly from year to year, less so from nest area to nest area. Overall reproductive rates in the two study areas differed only in 2000. We suggest that differences among the nest areas in reproductive rate likely indicate differences in habitat quality of individual nest areas, whereas differences among years likely reflect regional factors that influence nesting birds, such as weather.

Key words: Red-shouldered Hawk, Buteo lineatus, *Ohio*, *productivity*, *reproductive rate*, *suburban*, *urban*.

Variación Espacial y Temporal en Tasas Reproductivas de *Buteo lineatus* en Hábitats Suburbanos y Rurales en Ohio

Resumen. Medimos la tasa reproductiva de individuos de la especie *Buteo lineatus* que estaban anidando en el sudoeste suburbano de Ohio y en una región rural boscosa en Hocking Hills, sudeste de Ohio, desde 1997 hasta 2005. En la región suburbana, la tasa reproductiva varió enormemente entre nidos, pero varió menos de un año a otro, indicando que algunas áreas de anidación produjeron consistentemente más jóvenes que otras. El 25% más productivo de las áreas de anidación produjo el 44% de todos los pichones eclosionados, mientras que el 25% menos productivo produjo sólo el 7% de todos los pichones que eclosionaron. En el área rural, la tasa reproductiva varió significativamente de un año a otro, pero menos entre las áreas de anidación. Las tasas

reproductivas globales en las dos áreas de estudio sólo difirieron en 2000. Sugerimos que las diferencias en la tasa reproductiva entre las áreas de anidación probablemente indican diferencias en la calidad de hábitat de las áreas individuales de anidación, mientras que las diferencias entre años probablemente reflejan los factores regionales que influyen sobre las aves que anidan, como el clima.

The reproductive rate of raptors often varies from nest area to nest area (also called nesting territory; Steenhof and Newton 2007). Some nest areas are occupied consistently and regularly produce many young, whereas others are occupied irregularly and produce few young (Newton 1979, 1991, Korpimäki 1988, Kostrzewa 1996). In the Eurasian Sparrowhawk (*Accipiter nisus*), for example, Newton (1991) found that just a few females at particular nest areas were responsible for the production of most of the young in the area he studied.

Such variation in reproductive success by nest area has been attributed to variation in habitat quality, particularly prey availability (Newton 1979). In a few cases, variation in reproductive rate by nest area has been associated with a measure of habitat quality or prey availability. In a 17-year study in Scotland, Eurasian Sparrowhawks nesting in areas of higher quality laid eggs earlier and raised significantly more young than those at lower-quality sites (Newton 1991). Similarly, in a 9-year study, three species of woodland raptors were more successful and produced more young at high-quality territories than at low-quality territories (Kostrzewa 1996).

In short-term studies, however, it can be unclear whether consistently high reproductive rates are the result of some aspect of habitat quality such as prey abundance or of the quality of the adult birds breeding at that nest area. In long-term studies, in which we may be reasonably certain that the adult breeders have been replaced over the duration of the study, we may be more confident that any consistent differences in production are the result of habitat quality, although in some cases the quality of the nest area and the quality of the pair may not be independent, as the best birds may occupy the best areas (Newton 1979, Kostrzewa 1996).

Variability among nest areas in habitat quality and prey abundance may be high where habitats are fragmented and diverse (rather than homogeneous), and thus heterogeneous habitats are where we might expect to find significant variability among nest areas in reproductive rates. Cities and suburbs, with their fragmented habitats, multiple land uses, and heterogeneous management, contain the potential for great variation in nest-area quality and prey availability, hence reproductive rates in these regions might be expected to vary by nest area. Our objectives in this study were to determine whether reproductive rate varies by nest area in an urban/suburban population of Red-shouldered Hawks (*Buteo lineatus*) and to compare that rate to spatial and temporal variation in the reproductive rate of a population nesting nearby in a more homogeneous forested region.

METHODS

STUDY AREAS

Our suburban study area in southwestern Ohio ("SubSW" hereafter) is characterized by hilly, unglaciated terrain in the Interior Plateau ecoregion (Omernik 1987). Hills are dissected by many small streams through ravines and by two large rivers, the Great Miami and the Little Miami. Native upland forests are dominated by second-growth oak–hickory (*Quercus* spp., *Carya* spp.) and beech–maple (*Fagus grandifolia*, *Acer saccharum*) associations, with native riparian forests characterized by sycamores (*Platanus occidentalis*) and beech. Elevation ranges from approximately 140 to 270 m.

The SubSW study area consisted of Hamilton County, Clermont County, and southwestern Warren County, Ohio. The nests studied, however, were actually located in a wide band of suburban development surrounding the city of Cincinnati. Suburban areas varied from densely populated (residential lots approximately 20×35 m) to sparsely populated (>2.5-ha residential lots, as well as undeveloped private land). Human population density in the study area was approximately 480 people km^{-2}, based on population in the six suburban townships containing the greatest numbers of nests (Ohio Department of Development 2008, U.S. Census Bureau 2008). Most residences and other buildings were surrounded by lawns and other non-native vegetation, but residences tended to be located on level ground, with steep slopes and riparian areas left in native vegetation. Public land within the study area contained no residences but was used heavily for sports and other recreation. Land cover within Red-shouldered Hawk home ranges in the SubSW study area consisted, on average, of 41% forest, 50% residential, and 9% fields/pastures (Dykstra et al. 2001b).

The rural Hocking Hills study area ("RurHH" hereafter) is located in a hilly, unglaciated region within the Western Allegheny Plateau ecoregion in southeastern Ohio (Omernik 1987). This region contains numerous small high-gradient streams, one large river (the Hocking River), and many mid-size streams. Elevation ranges from approximately 200 to 310 m. Predominant forest type is oak–hickory. Drier sites are wooded with the chestnut oak (*Quercus prinus*) and black oak (*Q. velutina*), mesic slopes with the tulip-tree (*Liriodendron tulipifera*). 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*).

The RurHH study area consisted of Hocking County, eastern Vinton County, northern Athens County, and southern Perry County, including the Athens District of Wayne National Forest, Hocking State Forest, Zaleski State Forest, and associated private lands. Proximity to roads, houses, and other developed areas varied widely, with some areas containing residences, some recreational development such as picnic areas and trails, and some >1 km from any development. Land cover within the Wayne National Forest was 96% forest (USDA Forest Service 2006); however, private inholdings interspersed throughout the public land contained significantly more agriculture, pastures, and other open land. Human population density in the region was approximately 30 people km^{-2}, based on population in the four counties of the study area (Ohio Department of Development 2008, U.S. Census Bureau 2008).

NEST-LOCATION TECHNIQUES

We located nests primarily between mid-February and early April, prior to leaf-out, using several techniques (Dykstra et al. 2000). We searched near sites where Red-shouldered Hawks had responded to broadcasts of the species' calls in a related survey (Dykstra et al. 2001a) or where habitat appeared suitable (i.e., contained at least some mature forest). We searched historic nest areas (J. B. Holt, M. S. Woodrey, unpubl. data). We saw some nests from roads while traveling in the study areas, and, finally, interested biologists, birders, and landowners reported some nests or nest areas. In SubSW, members of a local raptor-rehabilitation association reported some nests to us. We found new nest areas in each year of the study.

Because Red-shouldered Hawks do not always reoccupy the same nest in successive years, it was often necessary to search for new nests within one nest area. Typically, conspecific calls were broadcast (Dykstra et al. 2001a) in the vicinity of the original nest; if one or more Red-shouldered Hawks were detected, we noted the direction from which the bird(s) responded and walked in that direction for up to 0.5 km while searching trees for stick structures. If we were unable to locate a new nest, we repeated the procedure 1–4 weeks later and also searched other forested portions of the nest area on foot. We considered a new nest found <0.5 km from a previously active nest to be within the same nest area. A nest found 0.5–0.8 km from a previously active nest was considered to be within the same nest area if that conclusion was supported by additional evidence (e.g., bird seen flying between the original and new nests, a lack of activity at the original nest in subsequent years, a temporal progression of new nests moving in that direction and indicating a shift of the nest area's boundaries).

MEASUREMENT OF REPRODUCTIVE RATE

We visited all known nest areas at least twice (and sometimes three or more times) between mid-February and mid-April, 1997–2005, and viewed nests from the ground using 8× or 10× binoculars or a 20–60× spotting scope. We considered nests to be active if there was evidence that eggs had been laid (i.e., incubating adult, small down feathers on the edges of nest, or broken eggshells below nest; Steenhof and Newton 2007). Nests found after the nestlings had hatched were not included in any analyses.

We climbed to most nests between 27 April and 19 June, 1997–2005, to count and band nestlings. Nestlings were counted as fledged if they were at least 3 weeks old, on the basis of the lengths of the first and second secondaries, according to Penak's (1982) age–feather length regression model for the Red-shouldered Hawk. At sites where nests were inaccessible, where permission to climb was denied, or where nestlings were <3 weeks old at banding, we viewed the nest from the ground when nestlings were well-grown (4.5–6 weeks) and counted the nestlings through a spotting scope.

We report the reproductive rate as the number of nestlings per active nest, as defined above. Measuring the reproductive rate only at nests where eggs were laid rather than at all nest areas with occupying pairs (regardless of whether they laid eggs) likely introduced some bias, because we excluded pairs that did not lay; these pairs had a lower reproductive rate and may have been in low-quality habitats. However, because Red-shouldered Hawks sometimes add nesting material to more than one nest during courtship (C. Dykstra and J. Hays, unpubl. data), and for other practical reasons (Steenhof and Newton 2007), we were able to obtain adequate reproductive information for the laying pairs only.

STATISTICAL ANALYSES

Because we wished to measure temporal as well as spatial variation in reproductive rates, we included nest areas in the analyses only if they were active in at least 4 of the 9 years of the study ($n = 71$ nests for SubSW and $n = 33$ for RurHH; Table 1). Because any single year's nest may fail due to random factors unrelated to territory quality (e.g., weather, isolated predation, or disturbance), 4 years of data provide a more accurate representation of reproductive success in a nest area than fewer years' data. Including only nests with at least 4 years of data minimized the influence of such events (Wiemeyer et al. 1984, 1993).

We used a mixed-model ANOVA (SPSS 2003) to analyze the variation in reproductive rate among nest areas within each study area. We used the univariate general linear model with the *random* statement, with year as the fixed effect and nest area as the random effect. We did not estimate the interaction of year *x* nest area because there were too few degrees of freedom.

We used Mann–Whitney *U*-tests for comparing the reproductive rates of the study areas for each year of the study. We calculated mean reproductive rate (number of young per active nest, 1997–2005) for each individual nest area and used linear regression to test whether mean reproductive rate was related to the number of years the nest area was active. We also calculated annual mean reproductive rate for each year in each study area and used a Wilcoxon rank-sum test to compare the two study areas' mean reproductive rates. Values reported in the text are means ± SE. We considered *P* values <0.05 to indicate a significant difference and $0.05 < P < 0.10$ to indicate a trend.

TABLE 1. Number of active Red-shouldered Hawk nests monitored per year in each study area in southern Ohio. Nests were considered active if there was evidence that eggs had been laid (i.e., incubating adult, small down feathers on the edges of nest, or broken eggshells below nest). Only nest areas active in at least 4 of the 9 years of the study are included here and in analyses.

Year	Study area	
	Southwestern Ohio	Hocking Hills
1997	19	8
1998	24	21
1999	41	23
2000	48	24
2001	56	22
2002	61	22
2003	58	22
2004	51	23
2005	58	22
1997–2005	71	33

RESULTS

SPATIAL AND TEMPORAL VARIATION
IN REPRODUCTIVE RATES

Southwestern Ohio suburban study area. In SubSW, the reproductive rate varied from nest area to nest area and may have varied from year to year (mixed-model ANOVA: for nest area, $F_{70,337} = 2.18$, $P < 0.001$; for year, $F_{8,337} = 1.76$, $P = 0.08$), indicating that some nest areas consistently produced more young than others. The mean number of young produced per year at individual nest areas ranged from 0.0 to 3.4 and was positively associated with the number of years the nest area was active ($F_{1,69} = 5.42$, $P = 0.02$; Fig. 1). The most productive 25% of nest areas produced 44% of all the nestlings in the study, whereas the least productive 25% of nest areas produced only 7% of all nestlings. Three nest areas produced 24, 27, and 31 young, respectively, in 9 years each. The annual reproductive rate of all nests in the SubSW study area ranged from 1.3 to 2.1 young per active nest, with a mean of $1.7 ± 0.1$ ($n = 9$ years; Fig. 2).

Hocking Hills rural study area. In RurHH, the reproductive rate did not vary significantly from nest area to nest area but did vary from year to year (mixed-model ANOVA: for nest area, $F_{32,146} = 1.35$, $P = 0.12$; for year, $F_{8,146} = 2.07$, $P = 0.04$). The number of young produced per year at individual nest areas ranged from 0.4 to 2.9 and was not related to the number of years the nest area was active ($F_{1,31} = 0.42$, $P = 0.52$). In RurHH, the most productive 25% of nest areas produced 40% of all nestlings, and the least productive 25% produced only 14%. The annual reproductive rate of all nests in the RurHH study area ranged from 1.0 to 2.5 young per active nest, with a mean of $1.6 ± 0.2$ ($n = 9$ years; Fig. 2).

COMPARISON BETWEEN STUDY AREAS

Total nestling production in the SubSW study area from 1997 to 2005 was 701 nestlings in 416 nesting attempts (1.7 young per active nest), whereas that at RurHH was 282 nestlings in 187 attempts (1.5 young per active nest). In 8 of the 9 years of the study reproductive rates in the two study areas did not differ ($P > 0.10$), but they may have differed in 2000 ($U = 420.5$, $P = 0.051$, $n = 24$ nests in RurHH, $n = 48$ nests in SubSW; Fig. 2). The mean annual
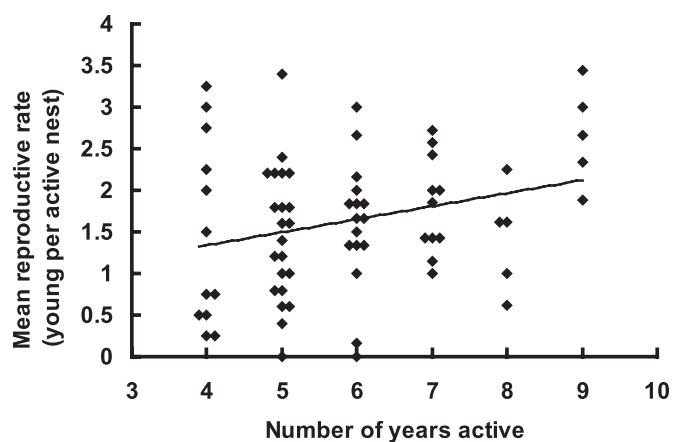

FIGURE 1. Mean reproductive rate of individual nest areas of Red-shouldered Hawks in suburban southwestern Ohio as a function of the number of years the nest area was active (i.e., eggs were laid). Only nest areas active in at least 4 of the 9 years of the study are included. Some markers have been slightly displaced horizontally for clarity.
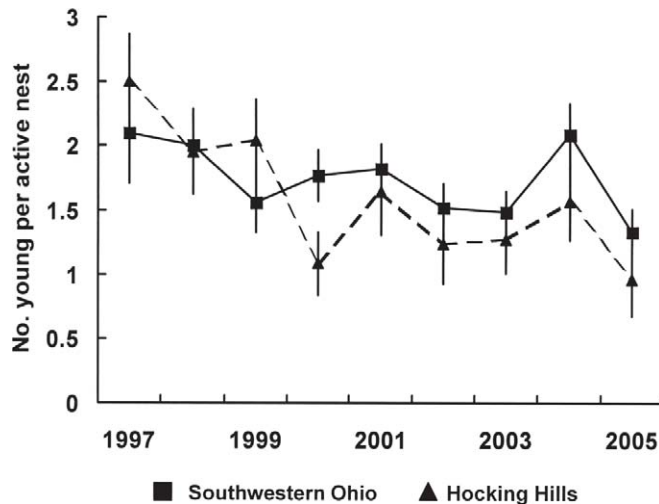
FIGURE 2. Mean (± SE) annual number of young per active nest of Red-shouldered Hawks at two study areas in southern Ohio, suburban southwestern Ohio (squares) and rural Hocking Hills (triangles). Nests were considered active if there was evidence that eggs had been laid. Only nest areas active in at least 4 of the 9 years of the study are included.

reproductive rate in SubSW and RurHH did not differ ($z = 1.125$, $P = 0.26$, $n = 9$ years).

DISCUSSION

SPATIAL VARIATION IN REPRODUCTIVE RATE

In the suburban southwestern Ohio study area, some nest areas consistently produced more young than others. Some nest areas never produced young, despite being active for 5–6 years (C. Dykstra and J. Hays, unpubl. data). As in the Eurasian Sparrowhawk (Newton 1991), a small percentage of the nest areas produced a disproportionately large number of the young. In addition, the mean reproductive rate of individual nest areas was positively correlated with the number of years the nest area was active, paralleling Newton's (1991) finding that breeding success of Eurasian Sparrowhawks is positively associated with the number of years a nest area is occupied. These two studies are not completely comparable because in our study new nests were found in each year, with the result that some nest areas were not searched in every year of the study; however, most nest areas in SubSW (65%) and RurHH (91%) were searched 7–9 years, minimizing any potential bias (C. Dykstra and J. Hays, unpubl. data).

In the rural, heavily forested Hocking Hills study area, there was a suggestion that reproductive rate might have been related at least weakly to nest area, although the relationship was not statistically significant. All nest areas in RurHH were successful in producing at least one young during the study, but the most productive RurHH nests did not produce as many young per year as the most productive SubSW nests. Thus, our data indicate that reproductive rate varied by nest area in SubSW and may also have varied by nest area in RurHH, although in the latter region the relationship was not as clearly detected in our dataset, possibly because of the smaller sample size at the RurHH study area.

Variation among nest areas in reproductive success is thought to be attributable to variation in habitat quality, of which the primary components are likely prey availability (Newton 1979) and

predator density (Sergio et al. 2003). Habitat quality, particularly in terms of prey availability, may be difficult to determine for the Red-shouldered Hawk because it is a dietary generalist (Dykstra et al. 2008). In SubSW, it consumes primarily small mammals, amphibians and reptiles but also takes birds, insects, and invertebrates (Dykstra et al. 2003); diet in the RurHH study area has not been determined quantitatively but likely differs little. Diet varies from region to region, however, and also from year to year within a study area (Bednarz and Dinsmore 1985, Townsend 2006), presumably with prey availability. Hence, measuring prey abundance at individual nest sites would be a formidable task, although an index to prey abundance at individual nest sites may be determined by measuring rates of prey delivery to nestlings.

Predator density may also be considered a component of habitat quality and may vary from nest area to nest area. In both SubSW and RurHH, primary predators of nesting Red-shouldered Hawks appear to be the Great Horned Owl (*Bubo virginianus*) and the Northern Raccoon (*Procyon lotor*; C. Dykstra and J. Hays, unpubl. data). In March 2008 in SubSW we recovered the carcass of a banded adult Red-shouldered Hawk in the nest of a Great Horned Owl (J. Hays, unpubl. data). Similarly, reproductive success of the Black Kite (*Milvus migrans*) in Italy was correlated with distance of the kite nest from the nearest nest of the Eurasian Eagle Owl (*Bubo bubo*), with kites <1 km from owl nests fledging no chicks (Sergio et al. 2003).

In other raptor species, variation between urban/suburban and rural sites in reproductive rates has been well documented. Millsap and Bear (2000) found reproductive rates of urban Burrowing Owls (*Athene cunicularia*) in Florida to be greater than those of birds in more rural regions, although the relationship reversed when residential development was very dense. Parker (1996) found urban Mississippi Kites (*Ictinia mississippiensis*) to have higher nest densities and produce more fledglings per nest attempt than rural ones. In contrast, Tella et al. (1996) found urban Lesser Kestrels (*Falco naumanni*) to have lower clutch sizes and reproductive rates than rural ones, even though predation rates on kestrel nests were lower at urban sites than at rural sites (Tella et al. 1996).

Variation among nest areas in reproductive rate may depend not only on the quality of the nest areas but also on the quality of the birds occupying the nest area (Newton 1991, Zollinger and Müskens 1994). In a short-term study, separation of these two factors may be difficult, but in a long-term study during which the nesting adults are replaced, any consistency in reproductive rates can be more easily attributed to habitat quality. During our 9-year study it is likely that at least one member of each pair was replaced at most nest areas, given that 95% of Red-shouldered Hawks banded as nestlings did not survive beyond 5.2 years (Dykstra et al. 2004), although the turnover rate of adults was unknown and at least one bird survived and nested on the same territory every year for the past 11 years (C. Dykstra and J. Hays, unpubl. data). Some studies, however, have found high-quality raptors both occupying the high-quality habitat and producing more young (Newton 1991). Thus habitat quality and bird quality are not independent, complicating analyses further.

TEMPORAL VARIATION IN REPRODUCTIVE RATES

Reproductive rates varied temporally at RurHH and perhaps at SubSW, although at the latter site the evidence was more uncertain. This difference suggested that regional variables that change from year to year, such as weather, had pronounced effects on only one of the study areas, RurHH, where such factors apparently were more significant determinants of reproductive rate than were differences among individual nest areas.

In a study similar to ours, McClaren et al. (2002) found that in the Northern Goshawk (*Accipiter gentilis*) reproductive rates varied temporally in each of three study areas but did not vary spatially by nest area within the study areas. The authors did not measure regional factors, such as weather and prey populations, but speculated that these factors may have accounted for the temporal variation in reproduction.

As a caveat, we note that we analyzed reproduction only for nest areas that were active (eggs were laid) at least 4 years of 9. Thus this dataset did not include the least successful nest areas, those occupied by pairs that did not lay eggs, and those where we found active nests fewer than 4 times in 9 years. Because our method may have limited us to only those nest areas that were the most suitable for breeding, it may represent the amount of variation among nest areas inaccurately. We contend that this potential bias did not unduly influence our results because we were able to document variation in reproductive rate among nest areas, even though our design and analytical constraints did not allow us to evaluate the entire population of Red-shouldered Hawks, which would have had a wider range of reproductive rates.

CONSERVATION

If only a few nest areas produce a disproportionately large number of the young, the population may be vulnerable to habitat loss and degradation, because if many of these most productive nest areas are destroyed or converted by habitat change to less productive sites, the population could decline rapidly. Alternatively, if the most productive nest areas are protected, management of this small portion of the total population could result in a disproportionate, positive effect on the population. However, identity of habitat features and other factors that make nest areas highly productive for Red-shouldered Hawks in our study areas requires further study.

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