BioOne COMPLETE

Colonization, Growth, and Density of a Pioneer Cooper's Hawk Population in a Large Metropolitan Environment

Authors: Stout, William E., and Rosenfield, Robert N.

Source: Journal of Raptor Research, 44(4) : 255-267

Published By: Raptor Research Foundation

URL: https://doi.org/10.3356/JRR-09-26.1

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 44 DECEMBER 2010 NO. 4

J. Raptor Res. 44(4):255–267
© 2010 The Raptor Research Foundation, Inc.

COLONIZATION, GROWTH, AND DENSITY OF A PIONEER COOPER'S HAWK POPULATION IN A LARGE METROPOLITAN ENVIRONMENT

WILLIAM E. STOUT[1]
W2364 Heather Street, Oconomowoc, WI 53066 U.S.A.

ROBERT N. ROSENFIELD
Department of Biology, University of Wisconsin–Stevens Point, Stevens Point, WI 54481 U.S.A.

ABSTRACT.—Cooper's Hawks (*Accipiter cooperii*) have recently colonized many urban landscapes across North America, but data on breeding densities and trends in densities of these populations are lacking. We surveyed for woodland raptors throughout approximately 1000 km^2 in the metropolitan Milwaukee, Wisconsin, area over a 21-yr period, 1988–2008. We documented the natural colonization of this urban landscape by a pioneer Cooper's Hawk population and its subsequent growth from 1993–2008 (4 to 41 laying pairs, 4 to 55 occupied sites). Nearest-nest distances decreased and the number of Cooper's Hawk laying pairs increased while nesting surveys remained consistent temporally and spatially, indicating that density of breeding pairs was increasing in the metropolitan Milwaukee area. Approximately 15 yr after initial colonization, the breeding density of Cooper's Hawks in some localized areas averaged one laying pair per 330 ha (range: 68–587 ha). From 1996–2008, as breeding density increased, average annual productivity (number of young/laying pair) for Cooper's Hawks in Milwaukee County, a subset of the overall larger metropolitan study area, also increased. During the early years of colonization, a relatively high proportion of individuals or pairs of birds appeared to occupy nest sites but did not breed. Younger birds may have played a role in the colonization of this urban landscape. This population was likely increasing at a relatively rapid rate during the late 1990s and continued to increase throughout the remainder of our study.

KEY WORDS: *Cooper's Hawk*; Accipiter cooperii; *colonization*; *pioneer population*; *population density*; *population trends*; *range expansion*; *raptor*; *urban.*

COLONIZACIÓN, CRECIMIENTO Y DENSIDAD DE UNA POBLACIÓN PIONERA DE *ACCIPITER COOPERI* EN UN AMBIENTE METROPOLITANO EXTENSO

RESUMEN.—La especie *Accipiter cooperii* ha colonizado recientemente muchos paisajes urbanos en América del Norte, pero no existen datos sobre las densidades poblacionales ni sobre las tendencias en éstas. Hicimos censos de aves rapaces de áreas arboladas a través de cerca de 1000 km^2 en el área metropolitana de Milwaukee, Wisconsin, a lo largo de 21 años (1988–2008). Documentamos la colonización natural de este paisaje urbano por parte de una población pionera de *A. cooperii* y su crecimiento subsiguiente entre 1993 y 2008 (de 4 a 41 parejas poniendo huevos, de 4 a 55 sitios ocupados). Las distancias al nido más cercano disminuyeron y el número de parejas con nidos aumentó, mientras que los censos de anidación fueron consistentes en el tiempo y espacio. Esto indica que la densidad de parejas reproductivas estaba aumentando en el área metropolitana de Milwaukee. Aproximadamente 15 años después de la colonización inicial, la densidad reproductiva de la especie en algunas áreas locales promedió una pareja poniendo huevos por cada 330 ha (rango: 68–587 ha). Entre 1996 y 2008, a medida que la densidad reproductiva

[1] Email address: stoutw@hotmail.com

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

aumentó, la productividad promedio anual (número de crías /pareja) de *A. cooperii* en el condado de Milwaukee (un subconjunto del área metropolitana mayor) también aumentó. Durante los primeros años de la colonización, una proporción relativamente alta de individuos o de parejas parecieron ocupar sitios de anidación pero sin reproducirse. Las aves relativamente jóvenes podrían haber jugado un papel en la colonización de este paisaje urbano. Esta población probablemente creció a una tasa relativamente rápida durante la parte final de la década de los noventa y continuó creciendo a lo largo del resto de nuestro estudio.

[Traducción del equipo editorial]

Generally, pioneer populations begin small with slow initial growth upon the colonization and occupation of new environs; they subsequently enter a relatively rapid growth phase, increase in density, and over time become well-established, stable populations (Newton 1998, Smallwood 2002, Rutz et al. 2006). Numerous studies have documented changes in avian population density as a result of experimentally induced variations in limiting factors such as food supply or nest-site availability (e.g., nest-site augmentation [nest box] programs; Newton 1998). The growth of the Peregrine Falcon (*Falco peregrinus*) population across the midwestern U.S. and Canada was the result of a large-scale reintroduction of this species (Tordoff and Redig 1997, Cade and Burnham 2003). However, few studies have investigated natural pioneer populations of avian species as they colonize new environments, particularly in urban landscapes. Oliphant and Haug (1985) documented expansion of the breeding range of a wild population of Merlins (*Falco columbarius*) as it colonized a new urban environment (Saskatoon, Saskatchewan, Canada), and Rutz (2008) studied wild Northern Goshawks (*Accipiter gentilis*) as they colonized the city of Hamburg, Germany, and reached a saturated, stable population. Stout et al. (2006a, 2007) investigated the status and nesting biology of a naturally occurring (wild), pioneer population of Cooper's Hawks (*A. cooperii*) in the Milwaukee, Wisconsin, area but did not report on growth or breeding density of this population.

Cooper's Hawks have colonized many urban environments across their breeding range in North America (e.g., Stahlecker and Beach 1979, Boal and Mannan 1999, Fish 2003). Some studies have suggested that urban habitats may serve as reproductive sinks for this species (Boal and Mannan 1998, Roth et al. 2005; but see Mannan et al. 2008). In contrast, long-term studies of urban populations of Cooper's Hawks in Wisconsin indicated that urban landscapes are not necessarily low-quality or inferior habitats (Rosenfield and Bielefeldt 2006, Stout et al. 2007, Stout 2009). Sweeney et al. (1997) suggested that raptors in urban landscapes may experience increased mortality because of anthropogenic interactions; however, Rosenfield et al. (2009) found that mortality of adult male Cooper's Hawks breeding in urban habitats did not differ from mortality of males breeding in rural locations.

Urban landscapes vary greatly in size, habitat heterogeneity, nest-site availability, prey populations, and other ecological factors that potentially affect breeding density and, hence, population status. Across North America, few studies have documented the demographics of urban Cooper's Hawk populations; in particular, little baseline information exists on abundance, breeding densities, and trends in densities (Rosenfield et al. 2007a, Stout et al. 2007). Thus, information on the breeding density of Cooper's Hawks inhabiting a variety of urban environments will enhance our ecological understanding of these populations (Rosenfield et al. 2007b, 2009, 2010, Stout et al. 2005). Such knowledge should form the basis for understanding the comparative ecology of Cooper's Hawks breeding in urban and rural settings across its broad North American range (*cf.* Boal and Mannan 1999).

The objectives of this study were to document the natural colonization of a pioneer Cooper's Hawk population, monitor its subsequent growth and reproduction, and determine how reproduction varied with time and density.

METHODS

Study Area. The metropolitan Milwaukee study area covers approximately 1000 km^2 in southeast Wisconsin (43°N, 88°W) and includes parts of Milwaukee, Waukesha, Washington, and Ozaukee counties (Fig. 1). Milwaukee County covers approximately 627 km^2 within this larger metropolitan area. The human population density within the city of Milwaukee is approximately 2400 people per km^2 (U.S. Census Bureau 2000). Landscape composition throughout the study area ranged from high-intensity urban land-use (high-density residential, commercial, or industrial) to low-intensity land-use in

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

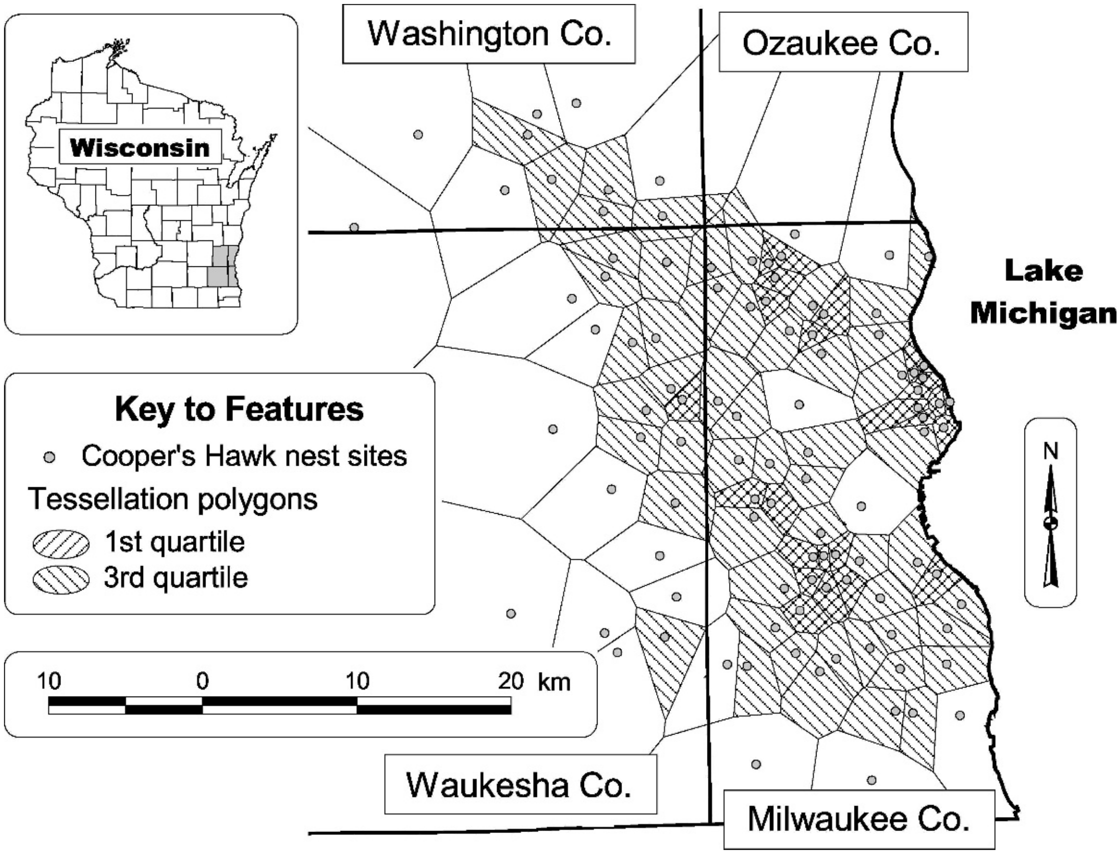

Figure 1. Dirichlet tessellation (i.e., Thiessen polygons) for Cooper's Hawk nest sites (1993–2008) in the metropolitan Milwaukee study area of southeast Wisconsin (43°N, 88°W). Tessellation polygon area metrics provided a minimum estimate of Cooper's Hawk breeding density.

suburban communities and rural agricultural areas (Stout et al. 2006b, 2006c). Remnants of historical vegetation were sparsely scattered throughout the study area; the size and abundance of these remnants increased along the urban–rural gradient (Matthiae and Stearns 1981, Stout 2004). Although conifers were sparsely scattered throughout this urban environment, the dominant vegetation primarily consisted of deciduous trees (Stout et al. 2006a).

Terminology. We followed Steenhof and Newton (2007) in defining a laying pair as a mated pair of birds that laid eggs (this constituted a breeding attempt); an occupied site as a nesting territory with an adult bird or a mated pair of birds (that do not necessarily lay eggs) that engaged in territorial defense, nest affinity, or other reproduction-related activity (includes laying pairs); a nest site as a breeding area or nesting territory that contained one or more nests within the home range of a pair of mated birds; and a successful pair as a mated pair of birds that raised at least one young to an advanced nestling stage (16–19 d, ca. 70% of fledging age; Stout et al. 2007). We considered an occupied site as a breeding attempt (i.e., a laying pair) if we observed an adult on the nest in an incubating posture. For this study we defined breeding density as the density of laying pairs within the Cooper's Hawk population. For all years in which we found Cooper's Hawk breeding attempts, we visited each nest at least twice (once at an early stage of incubation, and again when the young reached an advanced nestling stage) to determine reproductive success (Postupalsky 1974, Stout et al. 2007).

Nest Surveys. We found Cooper's Hawk nests incidentally from 1988–95 during intensive annual nesting surveys for Red-tailed Hawks (*Buteo jamaicen-*

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

sis) and Great Horned Owls (*Bubo virginianus*; Stout 2004, Stout et al. 2006b, 2006c). For these surveys, we located nests from a vehicle between 1 February and 30 April each year by driving major roads systematically so that we could view all suitable nest substrates before visibility was obscured by foliage (Stout et al. 2006b, 2006c). Vehicle routes were driven at least twice annually, and we checked woodlots that were not entirely visible from the road by foot. We continued to find Cooper's Hawk nests incidentally during the banding of Red-tailed Hawk nestlings, which extended into June, annually (1 May–21 June).

During 1996–2008, we specifically surveyed annually for Cooper's Hawk nests. To maintain objectivity, all surveys remained consistent both temporally and spatially across years (vehicle routes and times were comparable across years; time and distance averaged approximately 105 hr and 2230 km annually for these specific surveys; time and distance for surveys of other raptors which resulted in incidental detections averaged an additional 320 hr and 6630 km annually). We used the same two field personnel throughout our study years, and we did not augment surveys with broadcast calls. All nest sites were found in an objective manner while we followed specific survey routes. Each year we continued to find Cooper's Hawk nests incidentally while surveying along routes for other raptors (Stout et al. 2006a, 2007).

Cooper's Hawk nesting habitat within this study area varied greatly and included residential, industrial, commercial, and recreational (e.g., golf courses and parks of all sizes) land, cemeteries, other urban and suburban habitats, and natural woodland habitat (Stout et al. 2006a). Our surveys included a sampling of all habitat types within the urban landscape allowing an accurate estimate of annual breeding density over the study period (Stout et al. 2006a, 2007).

To aid in identifying nest sites of laying pairs, we monitored interyear presence and movements of marked adult (i.e., breeding) Cooper's Hawks that had been trapped near their nests from 1996 through 2008 (Stout et al. 2006a, 2007). We banded captured adult Cooper's Hawks with U.S. Geological Survey (USGS) lock-on aluminum leg bands and colored, alphanumerically coded leg bands. We banded nestlings at an advanced nestling age (16–19 d or about 70% of fledging age) with USGS lock-on aluminum leg bands. When resurveying areas where nests had been found in previous years, we searched within at least 400 m of nests from previous years and considered breeding attempts within this distance as the same nest site (Rosenfield et al. 1995). We considered breeding attempts beyond this distance as the same nest site only if we identified the breeding male by colored, alphanumerically coded leg band as the same male from a previous year and no other male was nesting within the resurveyed area (Rosenfield et al. 1995, Rosenfield and Bielefeldt 1996).

GIS Software and Procedures. All nests were mapped in the ArcView Geographic Information System (GIS) version 3.3 (Environmental Systems Research Institute [ESRI], Redlands, CA U.S.A.) using Southeast Wisconsin Regional Planning Commission (SEWRPC) ortho photos (1:4800 scale; grain: ca. 0.3 m) and vector GIS land-cover data (SEWRPC, Waukesha, WI U.S.A.; SEWRPC 2000, Stout et al. 2006c). We digitized 1993–2000 nest locations directly in the GIS, and we logged real-time Global Positioning System (GPS) locations for 2001–08 nests with an accuracy of 1–3 m using a Trimble GeoExplorer3 or GeoXT (Trimble Navigation Limited, Sunnyvale, CA U.S.A.). We differentially corrected the GPS location data to increase accuracy and used these locations to verify the accuracy of 1993–2000 nest locations. We used the Animal Movement Extension (Hooge and Eichenlaub 2000) to determine the central location (arithmetic mean based on nesting locations used in all years) of each nest site, to build a Dirichlet tessellation (i.e., Thiessen polygons) for nest sites, and to test for annual spatial dispersion patterns of nests. We used WGS (World Geodetic System) 1984 datum to calculate nearest-neighbor distances and US State Plane (1927, Wisconsin South 4083) projection for tessellation polygon analyses.

Population Density Metrics. We used nearest-nest (i.e., nearest-neighbor) distance and Dirichlet tessellation polygon area (for nest sites) metrics as indices of breeding density for this Cooper's Hawk population. For both metrics, we report first and third quartiles (25th and 75th percentiles of the frequency distribution of these two metrics, respectively; note: first quartile data are a subset of third quartile data; Hooge and Eichenlaub 2000, Krebs 1998). We use third quartile data as a reasonable approximation for the breeding density of Cooper's Hawks within the metropolitan Milwaukee study area, and first quartile data to represent a higher potential breeding density because we did not survey the entire study area completely (Fig. 1). We do not

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

report extreme values (i.e., >third quartile) because nest sites that we found represent a sample of all nest sites within the study area and nest sites with extreme values generally lie on the perimeter of the study area (Fig. 1).

For nearest-nest distance, we determined the distance from the nest of each laying pair to the nearest nest of adjacent pairs annually (calculated from GPS location data). We removed duplicate measures (i.e., two nests that were closest to each other and, therefore, had the same value) to maintain independence of samples. We considered nearest-nest distances for each nest site in different years as statistically independent observations. We used all independent nearest-nest distances (i.e., no duplicate measures) for each year from 1996–2008 to compare nearest-nest distances across the entire period. We did not include 1988–95 data (i.e., incidental nest detections) in this analysis or in other population density metrics (Fig. 2–4) because we did not specifically survey for nests in these years; thus, the two survey methods are not comparable. We calculated annual Cooper's Hawk breeding density from nearest-nest distances (for both first and third quartiles) based on Krebs (1998) and Byth and Ripley (1980). We also combined values across all years and report first and third quartiles for these combined nearest-nest distances.

For tessellation polygon areas, we used all Cooper's Hawk nests in which eggs were laid within each nest site across all years (1993–2008) to determine a central nest site location (arithmetic mean; Hooge and Eichenlaub 2000). We used these central nest site locations to build a Dirichlet tessellation (Fig. 1). For nest sites adjacent to Lake Michigan, we removed the area of coverage that extended over the lake from the tessellation polygons because water is not nesting habitat for these birds (Fig. 1). We report data for 26 first quartile nest sites (i.e., central nest site locations) and 79 third quartile nest sites.

We also present data on the Cooper's Hawk subpopulation that we found in Milwaukee County. We used these data to estimate annual breeding density within this defined area, a subset of the larger metropolitan Milwaukee study area. From these data, we assessed how productivity varied annually and with breeding density, and we tested for annual dispersion patterns of nests within this county during the years of consistent surveys (1996–2008). We did not assume that we found all nests within this defined area; however, our survey methods were consistent in this area and during this time period, as described above.

Statistical Analyses. We used linear regression to assess how annual first and third quartile nearest-nest distances for the metropolitan Milwaukee study area changed across time (1996–2008) and whether Cooper's Hawk population parameters for Milwaukee County varied over this same time period. We used SYSTAT (SYSTAT 10 for Windows; SPSS, Chicago, IL) for statistical analyses. We considered tests significant at $\alpha \leq 0.05$.

We used the Nearest Neighbor Analysis Test for Complete Spatial Randomness (Clark and Evans 1954, Hooge and Eichenlaub 2000) to determine annual spatial dispersion (clumped, random, or uniform) of nests for laying pairs within Milwaukee County from 1996–2008. Dispersion patterns provide insight into population density, habitat availability, and density limits (Newton 1998; also see Discussion). We report the range of R values for years with each dispersion pattern (Hooge and Eichenlaub 2000). An R value (range: 0–2) indicates how clustered or dispersed points are within a defined study area, with values near zero indicating a tendency toward a clumped dispersion, values near one indicating a random dispersion, and values near two indicating a uniform dispersion.

Results

Within the metropolitan Milwaukee study area, we found no breeding Cooper's Hawks (or occupied sites) from 1988–92 (presumed absence) and 4–9 laying pairs (4–15 occupied sites) annually from 1993–95 while surveying for other raptors (incidental detections). We found 20–41 Cooper's Hawk laying pairs (29–55 occupied sites) annually from 1996–2008 during the consistent nesting surveys. For the years of consistent surveys (1996–2008), mean annual nearest-nest distances decreased over time for both first and third quartile data (F = 13.220, df = 1 and 57, $P < 0.001$ and F = 78.777, df = 1 and 196, $P < 0.001$, respectively; Table 1, Fig. 2), and thus, breeding density estimates increased for both first and third quartile data (Table 1). Dirichlet tessellation polygons for Cooper's Hawk nest sites and, thus, breeding density estimates based on these polygons, averaged 330 and 806 ha per laying pair for first and third quartiles, respectively (Table 1).

The number of Cooper's Hawk laying pairs that we found in Milwaukee County increased from 13 in 1996 to 35 in 2008 (F = 92.911, df = 1 and 11, $P <$

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

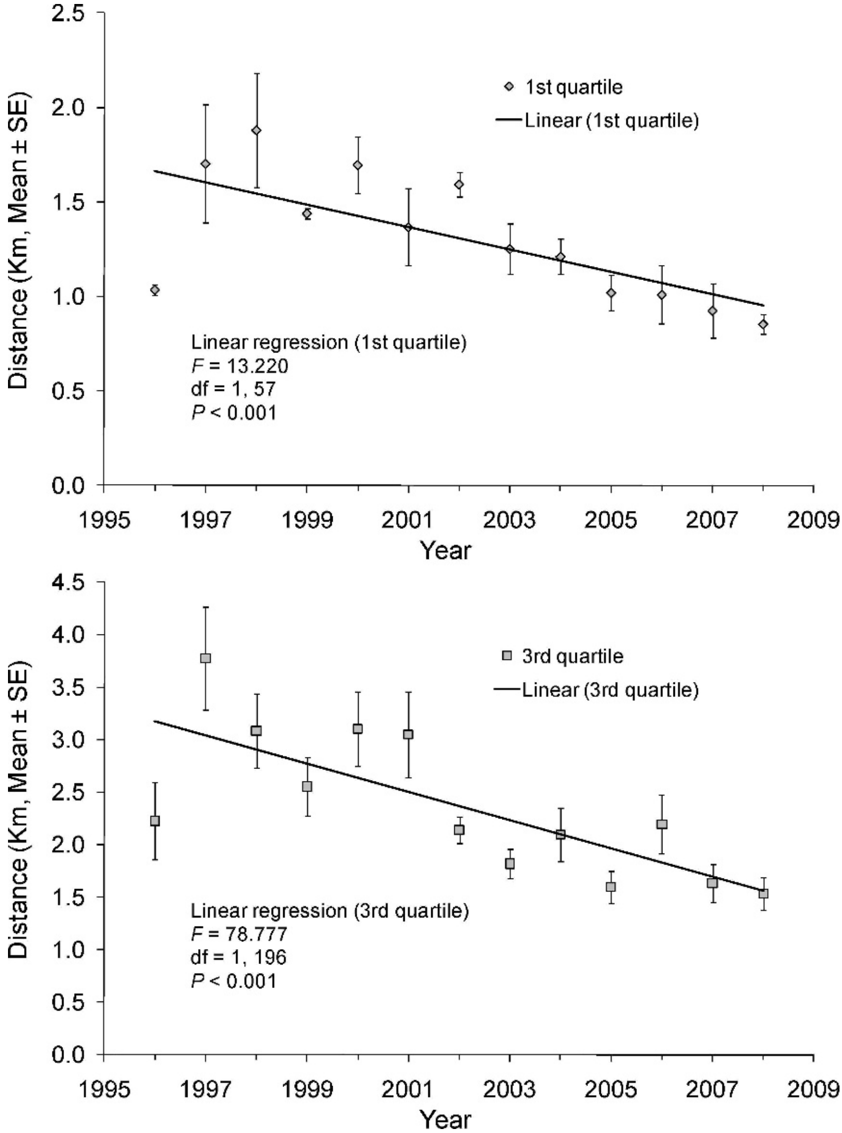

Figure 2. Nearest-nest distances for Cooper's Hawks in the metropolitan Milwaukee study area, 1996–2008. Mean annual nearest-nest distances decreased over this 13-yr period of consistent nesting surveys for both first and third quartiles. First and third annual quartiles are the 25th and 75th percentiles of the frequency distribution for nearest-nest distances, respectively (note: first quartile data are a subset of third quartile data).

0.001; Table 2, Fig. 3). During the early years of colonization, a relatively high proportion of individuals or pairs of birds appeared to occupy nest sites but did not breed (Table 2). Within Milwaukee County, average reproductive output for laying pairs of Cooper's Hawks increased over time and as breeding density increased (F = 19.232, df = 1 and 11, P = 0.001 and F = 14.916, df = 1 and 11, P = 0.003, respectively; Table 2, Fig. 4) across the 13-yr period (1996–2008; annual average = 2.3 young/laying pair, range: 1.9–3.0; Table 2). Annual spatial dispersion of Cooper's Hawk nests was random for all years from 1996–2008 (range for R: 0.83–1.18).

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

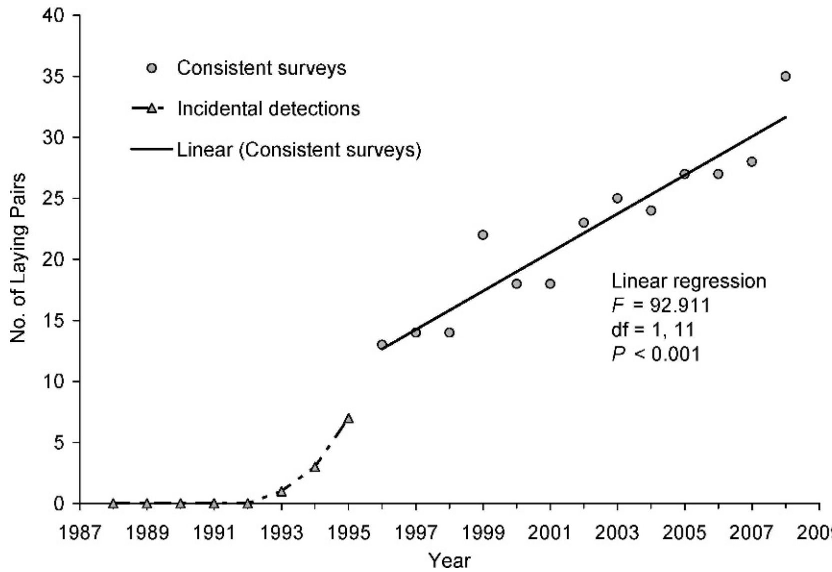

Figure 3. Number of Cooper's Hawk laying pairs in Milwaukee County found incidentally during intensive Red-tailed Hawk and Great Horned Owl nesting surveys, 1988–95, and found during consistent Cooper's Hawk nesting surveys, 1996–2008. The number of laying pairs within Milwaukee County increased during the consistent nesting surveys.

Discussion

Few studies have investigated pioneer populations of avian species as they colonize and increase in urban environments (Rutz 2008). Cooper's Hawks appeared to colonize the metropolitan Milwaukee area in the early to mid-1990s as a pioneer population, and subsequently this population expanded its range across the city. During the late 1990s and early to mid-2000s, this population was likely increasing at a relatively rapid rate. Reproductive output (number of young/laying pair) for Cooper's Hawks increased temporally and with increasing breeding density in Milwaukee County during this rapid growth phase.

We suggest that Cooper's Hawks breeding in the metropolitan Milwaukee area during 1993–95 comprised the initial pioneer population that subsequently entered a relatively rapid growth phase. During 1988–92, we found no Cooper's Hawks in the metropolitan Milwaukee area despite intensive nest searches. This initial five-year apparent absence and subsequent increases following initial detections during 1993–95 followed a pattern that was consistent with colonization (Fig. 3) as opposed to annual counts of laying pairs that fluctuate randomly or sporadically, which may suggest inadequate sampling. During the early years of colonization, a relatively high proportion of individuals or pairs of birds appeared to occupy nest sites but did not breed (e.g., 41% in 1996 for Milwaukee Co.; Table 2). This pattern was also observed for a pioneer population of Northern Goshawks (*A. gentilis*) in Germany (Rutz 2008). During the early years of our study, Stout et al. (2006a, 2007) found that the breeding population of Cooper's was relatively young based on a comparatively high but decreasing proportion of one-year-old breeders (particularly females); thus, they suggested that one-year-old breeders may have been important in establishing this pioneer population. Perhaps the initial colonizing population in our study was disproportionately comprised of younger birds because they could not find available nesting sites in saturated (i.e., high density), more traditional exurban Cooper's Hawk habitat. We suggest that, at the time of colonization, the metropolitan Milwaukee area was a novel urban landscape for these birds as we have no evidence to suggest that this population was recolonizing this urban environment; thus, this was a pioneer population. The presence of young breeders within our study population is also consistent with studies of pioneer populations of congenerics in Europe (Rutz et al. 2006, Rutz 2008) and other raptor populations that are not saturated (Newton 2003). Similarly, the role of young breeders in recolonization or establishing a pioneer population was proposed

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

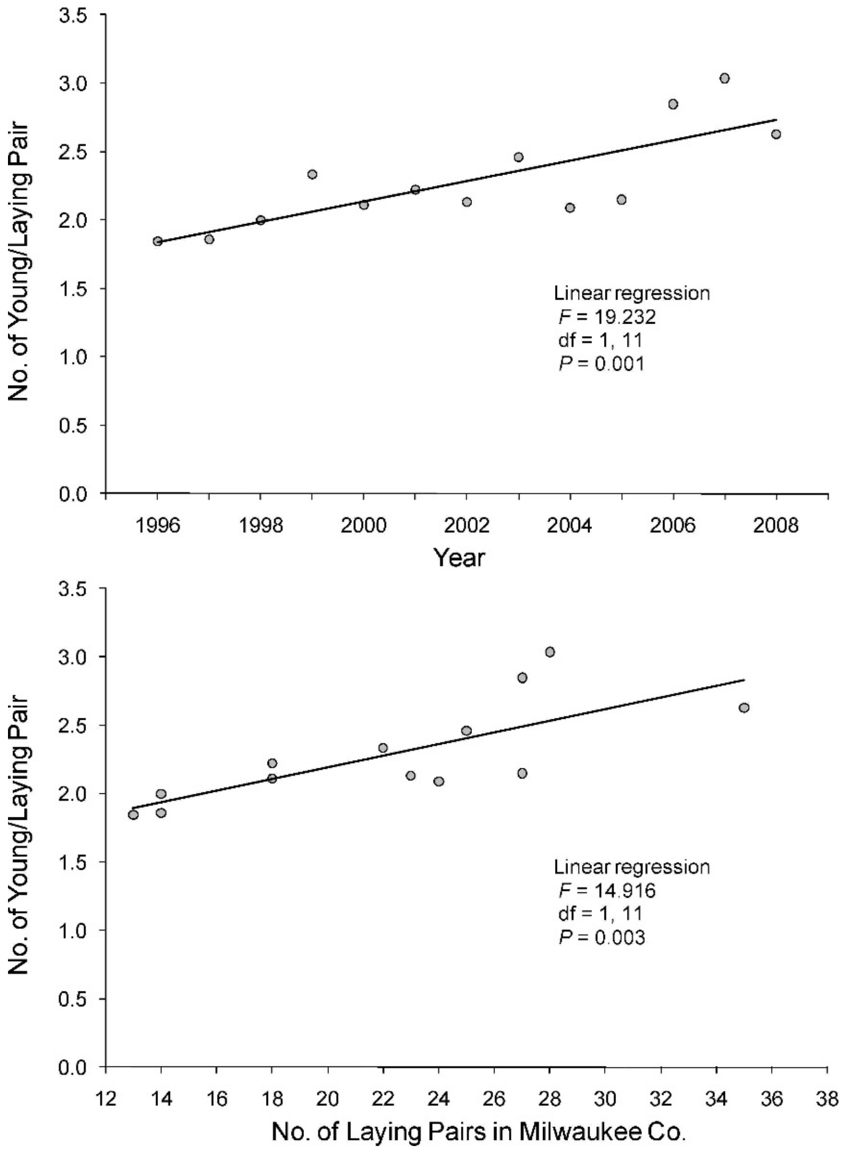

Figure 4. Density and annual reproductive output for nests of laying pairs of Cooper's Hawks in Milwaukee County, 1996–2008. Average annual productivity increased across this 13-yr period and with increased breeding density.

to explain the lag in occupation of historical rural habitats by the recently reestablished population of urban nesting Peregrine Falcons in the midwestern U.S. and Canada (Tordoff and Redig 2003).

Several studies suggested that avian species adapted in a rapid and dramatic fashion to urban environments in European cities (Kelcey and Rheinwald 2005). We estimate that in perhaps only one breeding generation, or six years (Rosenfield et al. 1995), the pioneer population of Cooper's Hawks in our study became established throughout the metropolitan Milwaukee area in a low-density, beginning growth phase. In less than two breeding generations, or 12 yr, this recently established population was widespread and increasing within the metropolitan Milwaukee area, likely in a relatively rapid growth phase. A similar pattern characterized a pioneer Merlin population in Saskatoon, Saskatchewan, Canada (Oliphant and Haug 1985, Sodhi et al. 1992). This population also had a relatively high

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1. Cooper's Hawk breeding population density metrics: nearest-nest distance and nest-site tessellation polygons.

		1st Quartile Nearest-nest Distances					1st Quartile Density[a]		3rd Quartile Nearest-nest Distances					3rd Quartile Density[a]	
Year	Total *N*	*N*	Mean	SE	Max	Min	Laying Pairs/ ha	Ha/ Laying Pair	*N*	Mean	SE	Max	Min	Laying Pairs/ ha	Ha/ Laying Pair
Nearest-nest distance[b]															
1993	3	0							2	6018	2237	8255	3781	0.00008	12 949.9
1994	3	0							2	9636	173	9808	9463	0.00003	29 179.3
1995	7	1	4280		4280	4280	0.00017	5756.2	5	5977	1209	10743	4280	0.00008	13 058.8
1996	14	3	1036	26	1072	985	0.00296	337.8	10	2228	370	4214	985	0.00051	1946.4
1997	19	4	1705	313	2402	885	0.00099	1005.2	14	3775	489	7261	885	0.00018	5456.2
1998	17	4	1882	303	2458	1315	0.00083	1198.8	12	3085	353	5170	1315	0.00029	3420.8
1999	23	5	1440	28	1502	1337	0.00153	652.2	17	2553	274	4666	1337	0.00041	2424.2
2000	19	4	1697	148	2117	1457	0.00108	925.7	14	3100	354	5494	1457	0.00028	3532.3
2001	18	4	1368	204	1789	815	0.00159	627.3	13	3049	404	5014	815	0.00028	3536.1
2002	18	4	1594	65	1744	1478	0.00125	802.6	13	2142	130	2782	1478	0.00066	1505.6
2003	19	4	1251	133	1475	898	0.00197	508.5	14	1819	138	2743	898	0.00090	1117.0
2004	21	5	1212	93	1461	959	0.00212	472.3	15	2093	255	3894	959	0.00060	1662.5
2005	21	5	1020	94	1270	711	0.00296	337.7	15	1597	152	2767	711	0.00111	903.1
2006	22	5	1010	153	1314	627	0.00286	349.8	16	2193	279	3779	627	0.00053	1878.7
2007	22	5	925	144	1315	575	0.00339	294.7	16	1632	179	3392	575	0.00101	987.7
2008	27	6	854	52	1082	741	0.00428	233.4	20	1534	152	2837	741	0.00114	878.0
All years	273	68	1221	35	1588	575	0.00203	493.3	204	2360	77	4634	575	0.00047	2129.8
Annual average			1520				0.00200	500.0		3277				0.00051	1973.4
Nest-site tessellation polygons[b]															
	106	26	329.6	33.0	587.2	67.5	0.00303	329.6	79	805.9	46.7	1711.9	67.5	0.00124	805.9

[a] Density estimates calculated from nearest-nest distances are based on Byth and Ripley (1980) and Krebs (1998).

[b] Mean, SE, max, and min values are in m for nearest-nest distances and ha for nest-site tessellation polygons.

percentage of young breeders (Oliphant and Thompson 1978, Warkentin et al. 1990) as it colonized the city rather quickly and subsequently entered a relatively rapid growth phase. The presence of a relatively high proportion of young (inexperienced) breeders in our study population may suggest especially favorable conditions (e.g., food availability) in the urban Milwaukee environment (Newton 1979; see below).

Reproductive output decreases as population density increases for some avian species, including raptors (Newton 1994, 1998, Rutz et al. 2006). However, average productivity for Cooper's Hawks in Milwaukee County increased with increasing breeding density, perhaps characteristic of a population in a relatively rapid growth phase. Boal (2001) found that adult laying pairs of Cooper's Hawks (i.e., after-second-year birds) had larger broods than laying pairs in which one or both breeders were one-year-old birds, a phenomenon also found in other raptor species (Newton 1979). Although Boal (2001) did not identify the urban population that he studied as a pioneer or young population, this phenomenon, in conjunction with the decreasing percentage of young breeders over time in our study (Stout et al. 2007) may, in part, explain the increasing productivity we found for this colonizing population.

Nest site availability and prey abundance and availability are external limiting factors that typically have the greatest impact on most raptor populations (Newton 1979, 1998, Rosenfield et al. 2007b). We hypothesize that neither nest site locations nor food were limiting Cooper's Hawk population growth in our study, environmental conditions generally associated with an increasing population. The number of individuals and overall biomass of avian prey are typically higher in urban environments compared to exurban environments (Marzluff et al. 1998, Rutz et al. 2006). The availability of safe nest sites and high prey abundance were considered to be the main reasons for the establishment of urban populations of

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Table 2. Cooper's Hawk population and reproductive output for Milwaukee County, Wisconsin.

Year	Occupied Sites[a]	Laying Pairs[b]	*N*	Productivity			Total Young
				Mean[c]	Max	Min	
Incidental detections[d]							
1988	0	0					
1989	0	0					
1990	0	0					
1991	0	0					
1992	0	0					
1993	1	1	1	2.00	2	2	2
1994	3	3	2	4.50	5	4	9
1995	8	7	6	2.83	5	0	17
Consistent surveys[d]							
1996	22	13	13	1.85	5	0	24
1997	19	14	14	1.86	4	0	26
1998	18	14	14	2.00	5	0	28
1999	25	22	21	2.33	5	0	49
2000	21	18	18	2.11	5	0	38
2001	25	18	18	2.22	6	0	40
2002	31	23	23	2.13	6	0	49
2003	30	25	24	2.46	6	0	59
2004	30	24	22	2.09	6	0	46
2005	33	27	27	2.15	5	0	58
2006	38	27	26	2.85	6	0	74
2007	42	28	28	3.04	6	0	85
2008	46	35	35	2.63	5	0	92
Total	380	288	283	2.36	6	0	668
Annual average	29.2	22.2	21.8	2.29			51.4

[a] A nesting territory with an adult bird or a mated pair of birds (that do not necessarily lay eggs) engaged in territorial defense, nest affinity, or other reproduction-related activity (includes laying pairs).
[b] A mated pair of birds that laid eggs, i.e., a breeding attempt.
[c] Number of young per laying pair.
[d] See Methods for a description of *incidental detections* and *consistent surveys.*

Merlins in Saskatoon, Saskatchewan (Sodhi et al. 1992, Warkentin et al. 2005) and Northern Goshawks in Hamburg, Germany (Rutz 2008). Breeding Cooper's Hawks in the metropolitan Milwaukee area appeared to rely predominantly on avian prey rather than mammals (W. Stout and R. Rosenfield unpubl. data). Thus, it is possible that abundance and availability of avian prey in the Milwaukee area may have influenced the colonization and growth of this Cooper's Hawk population. Nest site availability also may not have been limiting in our study area, as this population increased. Cooper's Hawks are known to use multiple types of pre-existing structures as nest substrates, including Red-tailed Hawk nests (Curtis et al. 2006, Stout et al. 2007). Stout et al. (1996, 2006c) suggested that Red-tailed Hawks were adapting to the urban environment in the metropolitan Milwaukee area because they used human-made structures as nest substrates. Although numerous Red-tailed Hawk nests existed on human-made structures (Stout et al. 1996, 2006c), Cooper's Hawks did not use these nests as base structures or build nests on human-made structures in this study area (Stout et al. 2006a). Based on the continued increase in the breeding Cooper's Hawk population and the fact that all nests were in natural substrates (i.e., trees), we hypothesize that typical nest sites were not limiting in this urban landscape.

The random dispersion patterns of nests we observed are consistent with the hypothesis that this population was not reaching density limits (i.e., saturated) as of 2008. Clumped and random disper-

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

sions may be the result of sequential filling of habitats (i.e., territory occupancy); specifically, nest sites with high-quality habitat are occupied first and, when the population is not saturated, low-quality habitat remains unoccupied (Newton 1998). Territorial species such as Cooper's Hawks tend to exhibit even dispersions when they reach density limits (Newton 1998, Rutz et al. 2006); however, the population we studied did not display even dispersion of nest sites in any year. Alternatively, an even dispersion may not be attainable in some urban environments with a wide variety of habitats (*cf.* Boal and Mannan 1998). If Cooper's Hawks use urban habitats disproportionately, a clumped dispersion may result. However, Cooper's hawks used a wide variety of urban habitats in the metropolitan Milwaukee area including residential, industrial, commercial, and recreational areas (Stout et al. 2006a). This finding is not surprising because recent evidence indicates that Cooper's Hawks can nest successfully in a wide array of urban and exurban habitats across its broad North American range (Nenneman et al. 2002, Rosenfield et al. 2007b, Mannan et al. 2008).

Tessellation polygon areas provide a reasonable approximation of Cooper's Hawk breeding density. Based on first quartile data, breeding density for some urban habitats in the metropolitan Milwaukee area averaged one laying pair per 330 ha (range: 68–587 ha). However, because we provide a sample of this breeding Cooper's Hawk population, not a complete survey, a higher density is likely, at least for some localized pockets of high-quality urban Cooper's Hawk habitat. Although home-range size and breeding density are not directly comparable, our higher breeding density estimates are consistent with estimates of home-range size for adult male Cooper's Hawks during the breeding season in other urban locations (Mannan and Boal 2000). Nevertheless, an accurate estimate of breeding density for Cooper's Hawks in Milwaukee may be difficult to determine because of the wide variety of urban habitats such as some of the larger areas of heavy urbanization. Some raptor studies suggest that urban populations may exceed density levels of rural populations (e.g., Gehlbach 1996). For Cooper's Hawks, Rosenfield et al. (1995) and Rosenfield and Bielefeldt (1996) documented a relatively high breeding density of one laying pair per 331 ha in rural southeast Wisconsin approximately 20 km west of the metropolitan Milwaukee study area; additionally, they found the highest known breeding density, one laying pair per 272 ha, in a suburban location in central Wisconsin in 1993. Based on first quartile nearest-nest distances, Cooper's Hawk breeding densities for localized areas within metropolitan Milwaukee appeared to reach or exceed comparable levels in 2008 (i.e., 233 ha per laying pair). The relatively high nesting densities reported for this growing urban population support our earlier suggestion that the metropolitan Milwaukee area is probably not a sink for nesting Cooper's Hawks (Stout 2006a, 2007).

Nest predation by raccoons (*Procyon lotor*) and Great Horned Owls may be the most widespread and important cause of nestling mortality (Curtis et al. 2006). For urban landscapes in the metropolitan Milwaukee area, raccoons were documented as nest predators of eggs, young, and adults; and Red-tailed Hawks and Great Horned Owls were also predators of both young and adults at nest sites (Stout et al. 2006a, 2007). Additionally, Stout et al. (2006a, 2007) suggested that predation at Cooper's Hawk nest sites did not differ in urban and rural locations. Thus, we hypothesize that reduced predation did not appear to be a factor in the colonization of this urban landscape by Cooper's Hawks, the subsequent relatively rapid growth of this population, or the increase in reproductive output of this population as breeding density increased. Furthermore, nest predation, in general, did not appear to impede this colonization.

Rutz (2008) noted a paucity of research documenting wildlife invasions of city environments and suggested that more detailed case studies are needed to advance our understanding of this phenomenon. Our study initially began as a result of incidental discoveries of Cooper's Hawk nests in a large metropolitan environment; and our research to date on the temporal dynamics of colonization, growth, and spatial distribution of this population has been largely descriptive (and pertains to a population that is still growing). We further note that many of our untested hypotheses regarding ecological influences of many parameters are in accord with findings and hypotheses of others. Like Rutz (2008), we urge testing of hypotheses regarding the ecological conditions that have prompted invasion and population growth of wildlife species in city environs.

Acknowledgments

W.G. Holton, J. Bielefeldt, J.M. Papp, Wisconsin Society for Ornithology (WSO) Breeding Bird Atlas field researchers, and others provided invaluable assistance. We greatly appreciated the gracious cooperation of all landowners for

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

allowing us access to their private lands. The WSO provided partial funding for this research annually through the WSO Small Grants Program (i.e., WSO Scholarship and Steenbock Award). J. Sukow, M.J. Gibson and Raptor Education Group provided additional support. The Personnel Development Committee and the Letters and Science Enhancement Fund at U.W.—Stevens Point provided partial funding for fieldwork; R.N. Rosenfield acknowledges sabbatical support of his campus. The Wisconsin Academy of Sciences, Arts and Letters—Project FIRST provided partial funding for the 1996–98 field seasons. D.E. Andersen, C.W. Boal, R.W. Mannan, C. Rutz, and four anonymous reviewers provided valuable comments that improved our manuscript.

LITERATURE CITED

BOAL, C.W. 2001. Nonrandom mating and productivity of adult and subadult Cooper's Hawks. *Condor* 103: 381–385.

——— AND R.W. MANNAN. 1998. Nest-site selection by Cooper's Hawks in an urban environment. *Journal of Wildlife Management* 62:864–871.

——— AND ———. 1999. Comparative breeding ecology of Cooper's Hawks in urban and exurban areas of southeastern Arizona. *Journal of Wildlife Management* 63:77–84.

BYTH, K. AND B.D. RIPLEY. 1980. On sampling spatial patterns by distance methods. *Biometrics* 36:279–284.

CADE, T.J. AND W.A. BURNHAM. [EDS.]. 2003. Return of the peregrine: a North American saga of tenacity and teamwork. The Peregrine Fund, Boise, ID U.S.A.

CLARK, P.J. AND F.C. EVANS. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453.

CURTIS, O.E., R.N. ROSENFIELD, AND J. BIELEFELDT. 2006. Cooper's Hawk (*Accipiter cooperii*). *In* A. Poole [ED.], The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY U.S.A., http://bna.birds.cornell.edu/bna/species/075.

FISH, A. 2003. Desperately seeking coops, the urban accipiter in Berkeley. Pacific Raptor Report No. 25. Golden Gate National Parks Conservancy, San Francisco, CA U.S.A.

GEHLBACH, F.R. 1996. Eastern Screech Owls in suburbia: a model of raptor urbanization. Pages 69–74 *in* D.M. Bird, D.E. Varland, and J.J. Negro [EDS.], Raptors in human landscapes. Academic Press, London, U.K.

HOOGE, P.N. AND B. EICHENLAUB. 2000. Animal movement extension to ArcView, version 2.0. Alaska Science Center—Biological Science Office, U.S. Geological Survey, Anchorage, AK U.S.A.

KELCEY, J.G. AND G. RHEINWALD. [EDS.]. 2005. Birds in European cities. Ginster Verlag, St. Katharinen, Germany.

KREBS, C.J. 1998. Ecological methodology, Second Ed. Addison Wesley Longman, Menlo Park, CA U.S.A.

MANNAN, R.W. AND C.W. BOAL. 2000. Home range characteristics of male Cooper's Hawks in an urban environment. *Wilson Bulletin* 112:21–27.

———, R.J. STEIDL, AND C.W. BOAL. 2008. Identifying habitat sinks: a case study of Cooper's Hawks in an urban environment. *Urban Ecosystems* 11:141–148.

MARZLUFF, J.M., F.R. GEHLBACH, AND D.A. MANUWAL. 1998. Urban environments: influences on avifauna and challenges for the avian conservationist. Pages 283–299 *in* J.M. Marzluff and R. Sallabanks [EDS.], Avian conservation: research and management. Island Press, Washington, DC U.S.A.

MATTHIAE, P.E. AND F. STEARNS. 1981. Mammals in forest islands in southeastern Wisconsin. Pages 55–66 *in* R.L. Burgess and D.M. Sharpe [EDS.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York, NY U.S.A.

NENNEMAN, M.P., R.K. MURPHY, AND T.A. GRANT. 2002. Cooper's Hawks, *Accipiter cooperii*, successfully nest at high densities in the Northern Great Plains. *Canadian Field-Naturalist* 116:580–584.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD U.S.A.

———. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70:265–276.

———. 1998. Population limitation in birds. Academic Press, San Diego, CA U.S.A.

———. 2003. The contribution of peregrine research and restoration to a better understanding of peregrines and other raptors. Pages 335–347 *in* T.J. Cade and W.A. Burnham [EDS.], Return of the peregrine: a North American saga of tenacity and teamwork. The Peregrine Fund, Boise, ID U.S.A.

OLIPHANT, L.W. AND E. HAUG. 1985. Productivity, population density and rate of increase of an expanding Merlin population. *Raptor Research* 19:56–59.

——— AND J.P. THOMPSON. 1978. Recent breeding success of Richardson's Merlin in Saskatchewan. *Raptor Research* 12:35–39.

POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Pages 21–31 *in* F.N. Hamerstrom, B.E. Harrell, and R.R. Olendorff [EDS.], Management of raptors. Raptor Research Report No. 2. Proceedings of the Conference on Raptor Conservation Techniques, Fort Collins, CO U.S.A.

ROSENFIELD, R.N. AND J. BIELEFELDT. 1996. Lifetime nesting area fidelity in male Cooper's Hawks in Wisconsin. *Condor* 98:165–167.

——— AND ———. 2006. Cooper's Hawk (*Accipiter cooperii*). Pages 162–163 *in* N.J. Cutright, B.R. Harriman, and R.W. Howe [EDS.], Atlas of the breeding birds of Wisconsin. Wisconsin Society for Ornithology, Madison, WI U.S.A.

———, ———, J.L. AFFELDT, AND D.J. BECKMANN. 1995. Nesting density, nest area reoccupancy, and monitoring implications for Cooper's Hawks in Wisconsin. *Journal of Raptor Research* 29:1–4.

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

———, ———, L.J. ROSENFIELD, A.C. STEWART, M.P. NENNEMAN, R.K. MURPHY, AND M.A. BOZEK. 2007b. Variation in reproductive indices in three populations of Cooper's Hawks. *Wilson Journal of Ornithology* 119:181–188.

———, ———, ———, T.L. BOOMS, AND M.A. BOZEK. 2009. Survival rates and lifetime reproduction of breeding male Cooper's Hawks in Wisconsin, 1980–2005. *Wilson Journal of Ornithology* 121:610–617.

———, J.W. GRIER, AND R.W. FYFE. 2007a. Reducing management and research disturbance. Pages 351–364 *in* D.M. Bird and K.L. Bildstein [EDS.], Raptor research and management techniques. Hancock House Publishers, Blaine, WA U.S.A.

———, L.J. ROSENFIELD, J. BIELEFELDT, R.K. MURPHY, A.C. STEWART, W.E. STOUT, T.G. DRISCOLL, AND M.A. BOZEK. 2010. Comparative morphology among northern populations of breeding Cooper's Hawks (*Accipiter cooperii*). *Condor* 112:347–355.

ROTH, T.C., II, S.L. LIMA, AND W.E. VETTER. 2005. Survival and causes of mortality in wintering Sharp-shinned Hawks and Cooper's Hawks. *Wilson Bulletin* 117: 237–244.

RUTZ, C. 2008. The establishment of an urban bird population. *Journal of Animal Ecology* 77:1008–1019.

———, R.G. BIJLSMA, M. MARQUISS, AND R.E. KENWARD. 2006. Population limitation in the Northern Goshawk in Europe: a review with case studies. Pages 158–197 *in* M.L. Morrison [ED.], The Northern Goshawk: a technical assessment of its status, ecology, and management. Studies in Avian Biology No. 31. Cooper Ornithological Society, Camarillo, CA U.S.A.

SEWRPC. 2000. SEWRPC 2000 land use codes. Southeast Wisconsin Regional Planning Commission (SEWRPC), Waukesha, WI U.S.A., http://www.sewrpc.org/regionallandinfo/metadata/sewrpc_2000_lu_codes.pdf (last accessed 12 February 2009).

SMALLWOOD, K.S. 2002. Habitat models based on numerical comparisons. Pages 83–95 *in* J.M. Scott, P.J. Heglund, M. Morrison, M. Raphael, J. Haufler, and B. Wall [EDS.], Predicting species occurrences: issues of scale and accuracy. Island Press, Washington, DC U.S.A.

SODHI, N.S., P.C. JAMES, I.G. WARKENTIN, AND L.W. OLIPHANT. 1992. Breeding ecology of urban Merlins (*Falco columbarius*). *Canadian Journal of Zoology* 70:1477–1483.

STAHLECKER, D.W. AND A. BEACH. 1979. Successful nesting by Cooper's Hawks in an urban environment. *Inland Bird Banding* 51:56–57.

STEENHOF, K. AND I. NEWTON. 2007. Assessing nesting success and productivity. Pages 181–192 *in* D.M. Bird and K.L. Bildstein [EDS.], Raptor research and management techniques. Hancock House Publishers, Blaine, WA U.S.A.

STOUT, W.E. 2004. Landscape ecology of the Red-tailed Hawk: with applications for land-use planning and education. Ph.D. dissertation, University of Wisconsin, Madison, WI U.S.A.

———. 2009. First documented eight-egg clutch for Cooper's Hawks. *Journal of Raptor Research* 43:75–76.

———, R.K. ANDERSON, AND J.M. PAPP. 1996. Red-tailed Hawks nesting on human-made and natural structures in southeast Wisconsin. Pages 77–86 *in* D.M. Bird, D.E. Varland, and J.J. Negro [EDS.], Raptors in human landscapes. Academic Press, London, U.K.

———, A.G. CASSINI, J.K. MEECE, J.M. PAPP, R.N. ROSENFIELD, AND K.D. REED. 2005. Serologic evidence of West Nile virus infection in three wild raptor populations. *Avian Diseases* 49:371–375.

———, R.N. ROSENFIELD, W.G. HOLTON, AND J. BIELEFELDT. 2006a. The status of breeding Cooper's Hawks in the metropolitan Milwaukee area. *Passenger Pigeon* 68: 309–320.

———, ———, ———, AND ———. 2007. Nesting biology of urban Cooper's Hawks in Milwaukee, Wisconsin. *Journal of Wildlife Management* 71:366–375.

———, S.A. TEMPLE, AND J.R. CARY. 2006b. Landscape features of Red-tailed Hawk nesting habitat in an urban/suburban environment. *Journal of Raptor Research* 40:181–192.

———, ———, AND J.M. PAPP. 2006c. Landscape correlates of reproductive success for an urban–suburban Red-tailed Hawk population. *Journal of Wildlife Management* 70:989–997.

SWEENEY, S.J., P.T. REDIG, AND H.B. TORDOFF. 1997. Morbidity, survival and productivity of rehabilitated Peregrine Falcons in the upper midwestern U.S. *Journal of Raptor Research* 31:347–352.

TORDOFF, H.B. AND P.T. REDIG. 1997. Midwest Peregrine Falcon demography, 1982–95. *Journal of Raptor Research* 31:339–346.

——— AND ———. 2003. Peregrines in the midwest. Pages 173–187 *in* T.J. Cade and W.A. Burnham [EDS.], Return of the peregrine: a North American saga of tenacity and teamwork. The Peregrine Fund, Boise, ID U.S.A.

U.S. CENSUS BUREAU. 2000. U.S. Census 2000. U.S. Dept. of Commerce, Washington, DC U.S.A., http://www.census.gov/main/www/cen2000.html (last accessed 12 February 2009).

WARKENTIN, I.G., P.C. JAMES, AND L.W. OLIPHANT. 1990. Body morphometrics, age structure, and partial migration of urban Merlins. *Auk* 107:25–34.

———, N.S. SODHI, R.H.M. ESPIE, A.F. POOLE, L.W. OLIPHANT, AND P.C. JAMES. 2005. Merlin (*Falco columbarius*). *In* A. Poole [ED.], The birds of North America online. Cornell Lab of Ornithology, Ithaca, NY U.S.A., http://bna.birds.cornell.edu/bna/species/044.

Received 24 April 2009; accepted 9 July 2010
Associate Editor: Joan L. Morrison

Downloaded From: https://bioone.org/journals/Journal-of-Raptor-Research on 25 Apr 2024
Terms of Use: https://bioone.org/terms-of-use