Wilson Bull., 94(1), 1982, pp. 31–45

NEST-SITES AND HABITAT OF RED-SHOULDERED AND RED-TAILED HAWKS IN IOWA

JAMES C. BEDNARZ AND JAMES J. DINSMORE

Numerous studies have addressed the breeding biology of the Red-tailed Hawk (*Buteo jamaicensis*) (referred to as RTH) (e.g., Fitch et al. 1946, Orians and Kuhlman 1956, Luttich et al. 1971, Seidensticker and Reynolds 1971, Gates 1972, McInvaille and Keith 1974, Johnson 1975, Petersen 1979), and the Red-shouldered Hawk (*B. lineatus*) (referred to as RSH) (Stewart 1949, Henny et al. 1973, Wiley 1975, Portnoy and Dodge 1979). However, only a few studies (Campbell 1975, Howell et al. 1978) have quantified some parameters of nesting habitats of RSH and RTH. Recently, Titus and Mosher (1981) quantitatively examined the nest-sites of four sympatric woodland hawks (including RSH and RTH) in the central Appalachians. Here we describe nest-sites and examine habitat partitioning of nesting RSH and RTH in Iowa.

STUDY AREA AND METHODS

Fieldwork was done during the spring and summer of 1977 and 1978. Most nests studied were in northeastern Iowa, but data also were collected from four RTH nest-sites in central Iowa. Intensive agriculture (corn, soybeans, cattle feedlots) is the dominant land use in both areas. Most hawk nests were along rivers and streams where cropland interdigitated with woodland and pasture. This land has steep topography or intermittently flooded bottomlands and is unsuitable for row crops. Nest searches following the methods of Craighead and Craighead (1956) were done in both forested bottomlands and upland habitats. All RSH nests found were in floodplain forests dominated by silver maple (*Acer saccharinum*), American elm (*Ulmus americana*) and cottonwood (*Populus deltoides*). Red-tailed Hawk nests were found both in floodplains and upland oak (*Quercus* sp.)-hickory (*Carya* sp.) communities.

Nest tree height and nest height were measured with a rangefinder. Slope of ground supporting the nest tree was determined with an oblique distance pendulum. Diameter of branches supporting nests and nest diameter were recorded for 22 nests climbed in 1978 and two 1977 RSH nests.

The quadrat and point-centered quarter methods were used to quantify vegetation at 38 nest-sites (Mueller-Dombois and Ellenberg 1974). Quadrats consisted of a 730-m^2 circle (radius = 15.24 m) centered on the nest tree. Four 64-m point-quarter transects following the cardinal directions were run from each nest tree. Twenty-nine points were sampled at each nest-site; one at the nest tree and seven (spaced 9.14 m) on each transect. If the transect entered a clearing, point-quarter transects were continued only to the last point where trees could be measured. Diameter at breast height (dbh) was measured and tree density was calculated for all trees greater than 5 cm dbh. These measures are referred to as quadrat dbh, quadrat density, point dbh and point density.

Other variables examined in the nest-site analysis were (1) tree-nest difference—nest tree height minus nest height in meters, (2) slope aspect—direction exposure of slope (N, NE, E, SE, S, SW, W, NW), (3) nest location—on main trunk crotch, on principal branch crotch, braced against trunk with smaller branches, leaning straight branch, or overhanging branch (crotch—a vertically oriented three or more branch juncture on the main trunk or principal branch capable of supporting a buteo nest), (4) nest-trunk difference—distance between nest and main trunk estimated in meters, (5) branch class—number of branches supporting nest with diameter $\leq$5 cm (A), >5 cm but $\leq$10 cm (B), or >10 cm (C) (estimated from ground), (6) canopy cover—canopy cover at nest height in percent (estimated: 0, 5, 10, 20, 30, 40, or 50%), (7) mean nest diameter—(longest + shortest diameter)/2 in meters, (8) mean support branch diameter—mean diameter of branches supporting nest in cm, (9) woodlot size—nesting woodlot size in ha (determined from a cover map using a planimeter), (10) nest openness—mean arc distance between nest support branches, calculated as (nest circumference − sum of diameters of support branches)/no. of support branches, and (11) tree density at nest height—estimated by using regression analysis to determine the number of trees reaching nest height within each 730-m^2 nest quadrat and recorded as no./ha (see Bednarz 1979).

Data were collected at 26 RTH, and eight active and four inactive (alternate or abandoned) RSH nest-sites. Sample size is not equal for all variables because several nest trees could not be climbed, and one inactive nest blew down before a complete data set was collected. Variables used in the microhabitat nest-site discrimination analysis were nest tree height, tree-nest difference, nest tree dbh, slope, nest location, nest-trunk difference, number of nest support branches, branch class A (percent), branch class B (percent), mean nest diameter, mean supporting branch diameter, nest openness, tree density at nest height, quadrat density, quadrat dbh, and woodlot size.

Cover maps were drawn from 1969–1971 aerial photos at 38 nest-sites. Maps were updated in the field. A compensating polar planimeter was used to measure the areas of cover types within a 1-km radius (314-ha circle) of each nest. Distance of woodland edge along potential nonforested hunting habitat (pastures, marshes, prairie, etc.) was measured with a map measuring wheel. Neither species was observed foraging in cropland and, therefore, this habitat type was not considered potential hunting habitat. The mean maximum diameters of 34 red-shoulder and 16 red-tail ranges were 1.4 and 2.8 km, respectively (calculated from Craighead and Craighead 1956:258–263). Therefore, the 2-km diameter used here should include most of the range used at each nest.

Variables included in the habitat discriminant analysis were upland forest area, marsh area, upland hunting area, number of separate hunting areas, mean size of hunting areas, human use area, cropland area, and edge. Floodplain forest area was negatively correlated with upland forest and cropland and was discarded by the stepwise discriminant procedure.

The data were tested univariately with Student's t-tests, chi-square tests, and analysis of variance (Snedecor and Cochran 1967); multivariate analysis of nest-site and habitat data was done with discriminant function and profile analyses (Morrison 1976). Data on slope aspects of nests were tested with the Kolmogorov-Smirnov test. Values presented after means are standard deviations. Computer analyses were done with SAS (Statistical Analysis System, Barr et al. 1976) and BMDP (Biomedical Data Package–1977; Health Sciences Computing Facility, University of California–Los Angeles) program packages.

RESULTS AND DISCUSSION

Nest-sites and nests.—We found 12 Red-shouldered Hawk nests in four different tree species and 24 Red-tailed Hawk nests in nine different tree species. Buteos are thought to select nest trees in relation to the availability of large trees (Dixon 1928, Bent 1937). Howell et al. (1978) reported that species of nest trees used by RTH were correlated with tree impor-

TABLE 1
COMPARISON OF RED-SHOULDERED AND RED-TAILED HAWK NEST-SITE CHARACTERISTICS

	Red-shouldered Hawk		Red-tailed Hawk		
Variable	N	Mean ± SD	N	Mean ± SD	Probability[a]
Nest height (m)	11	19.1 ± 4.8	26	17.1 ± 4.2	0.2035
Nest tree height (m)	12	28.6 ± 4.6	26	22.1 ± 5.1	0.0006**
Tree–nest difference (m)	11	9.2 ± 1.9	26	5.0 ± 3.0	<0.0001**
Nest tree dbh (cm)	12	63.0 ± 12.7	26	48.9 ± 12.9	0.0031*
No. of support branches	11	3.6 ± 0.5	27	3.7 ± 1.3	0.6891
Nest–trunk difference (m)	11	0.3 ± 0.8	26	0.7 ± 1.2	0.2381
Canopy cover (%)	12	27.5 ± 12.9	26	12.2 ± 11.8	0.0009**
Mean supporting branch diameter (cm)	7	17.2 ± 6.6	18	8.9 ± 3.0	0.0126*
Mean nest diameter (cm)	7	57.1 ± 8.4	17	68.2 ± 10.0	0.0169*
Nest openness (cm)	7	33.8 ± 9.0	17	55.6 ± 14.7	0.0015*
Slope (degrees)	12	0.1 ± 0.3	26	17.2 ± 12.3	<0.0001**
Tree density at nest height (#/ha)	11	161.9 ± 68.1	26	118.7 ± 71.1	0.0961

[a] Student's *t*-test.
* Significant ($P < 0.05$); ** significant ($P < 0.001$).

tance values (sum of relative density, the relative frequency and the relative basal area). Perusal of 44 papers on nesting RSH revealed that 40 species have been used as nest trees, suggesting that species is relatively unimportant in nest-site selection.

RTH nests typically were in smaller trees, closer to the tops of trees, in areas of less canopy cover, had greater nest openness, and more often were placed in trees on slopes than RSH nests (Table 1). Nest openness of only three RTH nests overlapped the range of RSH. Two of these nests were unsuccessful; one had been deserted for several days preceding measurement, and had weathered. The nest openness of the successful nest was only 0.02 cm smaller than the largest RSH nest. By placing their nests high in trees on slopes, RTH in Iowa may have improved access because the canopy of trees downslope of the nest does not reach nest height. Although the limited number of trees on level ground may force many Iowa RTH to nest on forested slopes, all nests on slopes we examined had at least some nesting trees on near-level ground available nearby.

RTH nests are larger than RSH nests, but are located on smaller support branches (Table 1). RSH located their nests either on a main trunk crotch (86%) or on a main branch crotch (14%). RTH constructed nests in all locations (see Methods), most commonly braced by small branches against the main trunk (38%). The tendency for RSH to place nests on a main

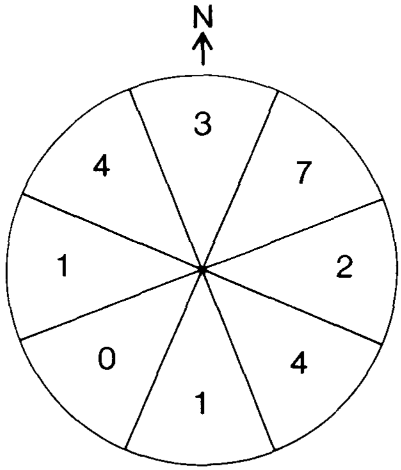

FIG. 1. Direction aspect of 22 Iowa Red-tailed Hawk nests located on hillsides.

trunk crotch more often than RTH was significant ($\chi^2 = 8.6$, df = 1, $P < 0.01$). Previous workers also noted that red-shoulders primarily built nests in secure tree crotches (Bent 1937, Stewart 1949).

Most streams in the study area drain to the southeast. Therefore, most available slope aspects are northeast and southwest. RTH tended to avoid placing nests on southwest facing slopes (Fig. 1), but this result was not significant ($P = 0.17$, Kolmogorov-Smirnov test), possibly because of small sample size. In addition, the single nests located on west and south facing slopes were unsuccessful. Hawk nests on southwest facing slopes are exposed to higher temperatures and greater insolation (Geiger 1965:369–393), perhaps causing heat stress in the young. Mosher and White (1976) thought that Golden Eagles (*Aquila chrysaetos*) selected cliff nests oriented to reduce direct insolation and thermal stress.

The two hawk species differed significantly in four general habitat features (Table 2). RSH were associated with large woodlots and built their nest close to water, but seemed to avoid buildings and roads. We believe that woodlot size is the most important variable. Many workers have reported that RSH nest primarily in larger woodlots (Bent 1937, Stewart 1949, Henny et al. 1973, Campbell 1975). Conversely, RTH generally inhabit more open habitats and will nest in fencerows or isolated trees (Hagar 1957, Bock and Lepthien 1976).

RSH often are associated with open water (Hahn 1927, Dixon 1928, Wiley 1975, Titus and Mosher 1981). This species probably is not depen-

TABLE 2
COMPARISON OF RED-SHOULDERED AND RED-TAILED HAWK NEST LOCATIONS IN RELATION TO WOODLOT SIZE AND DISTANCE TO NEAREST WATER, BUILDINGS AND ROADS

Variable	Red-shouldered Hawk		Red-tailed Hawk		Probability of a larger t value[a]
	N	Mean ± SD	N	Mean ± SD	
Woodlot size (ha)	12	98 ± 65	26	47 ± 44	0.0076*
Distance to water (m)	12	142 ± 120	26	522 ± 571	0.0030*
Distance to road (m)	12	820 ± 509	26	309 ± 233	0.0054*
Distance to building (m)	12	1001 ± 510	26	495 ± 218	0.0058*

[a] Student's t-test.
* Signficant ($P < 0.05$).

dent on water per se, but rather, is adapted to the forested floodplain consisting of level woodlands interspersed with small marshes and backwater channels created by flowing water.

RTH nested closer to buildings and roads than did red-shoulders (Table 2). This seems a consequence of the habitat in Iowa. RTH primarily used open farmland areas which are associated with roads and buildings; RSH were found in the bottomland habitats of wildlife refuges and parks with few roads and buildings. Campbell (1975) found RSH nesting in woodlots near busy highways and ongoing land-development projects.

The discriminant analysis of 13 variables that exhibited differences or represented important characteristics of the nest-site microhabitat (see Methods) correctly classified all 37 nest-sites to the proper species (Fig. 2).

Mean nest diameter, mean supporting branch diameter and nest openness were recorded at only 23 of the 37 nest-sites and could not be included in the analysis of the total sample. These three variables were included in a second discriminant analysis with a smaller sample. Branch classes A and B were deleted from the second analysis because they duplicated the variable mean supporting branch diameter. Again, all nest-sites were properly classified (Fig. 3). The single RSH outlier had the largest nest openness and the greatest mean supporting branch diameter (Fig. 3).

For each analysis, the six variables with the best discrimination power, ranked according to the discriminant coefficients, generally are related directly to nest accessibility (Table 3).

Natural selection of a species' nest-site preference is related to many factors such as providing safety from predators and weather, adequate access to nest, proper support, site availability and adequate area for adults and young. This study shows that red-tail nests are characterized

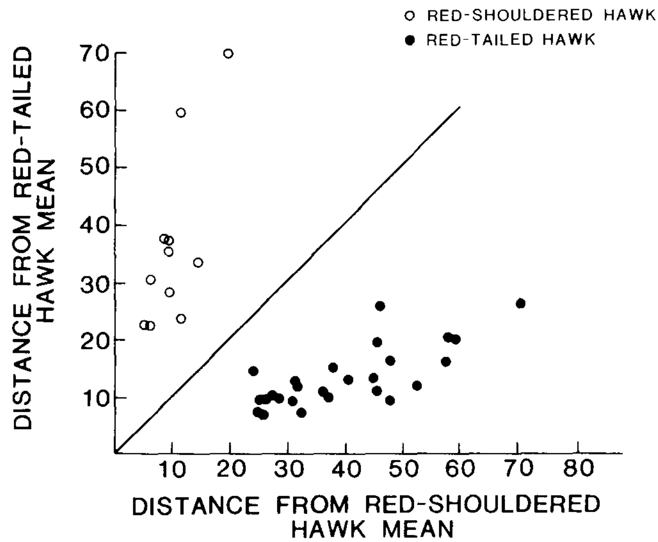

FIG. 2. Discriminant analysis of 11 Red-shouldered and 26 Red-tailed hawk nest-sites graphically represented by Mahalanobis distances from the respective means.

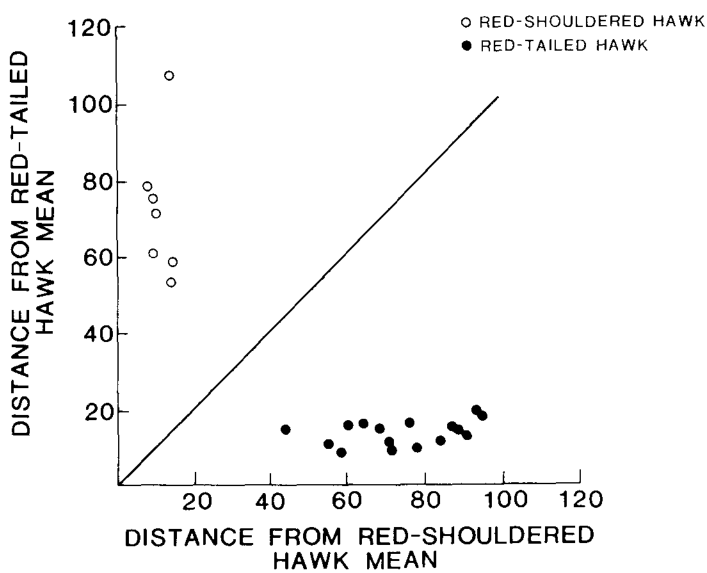

FIG. 3. Discriminant analysis of seven Red-shouldered and 16 Red-tailed hawk nest-sites graphically represented by Mahalanobis distances from the respective means.

TABLE 3

THE SIX MOST IMPORTANT VARIABLES IN THE CLASSIFICATION OF RED-SHOULDERED AND RED-TAILED HAWK NEST-SITES RANKED ACCORDING TO DISCRIMINANT COEFFICIENTS

Discriminant analysis of 37 nest-sites		Discriminant analysis of 23 nest-sites	
Variable	Discriminant coefficient	Variable	Discriminant coefficient
Slope	0.78	Quadrat density	1.30
Tree density at nest height	0.63	Nest openness	1.20
Nest location	0.52	Slope	1.14
Tree–nest difference	0.50	No. of support branches	1.06
Quadrat density	0.38	Quadrat dbh	0.97
Nest tree height	0.37	Tree–nest difference	0.81

by high accessibility. Red-tail nests are built high in trees, on small support branches, located in lower density forests, in areas of less canopy cover and more often in a tree on a slope (Tables 1, 2) than RSH nests. This accessibility makes nests vulnerable to storm damage and increases exposure to direct sunlight and temperature extremes, which can be stressful to young raptors (Mosher and White 1976). Additionally, red-tails construct relatively large nests on small branches (Table 1). We believe it is unlikely that space needed for young has led to the evolution of the present large diameter RTH nest. All RTH nests we examined seemed to provide more than adequate space for the young compared to obviously crowded RSH nests with as many as four young. Alternatively, we suggest that one possible function of the large diameter nest is to improve nest access.

Seemingly, Red-tailed Hawks also increase nest accessibility by placing nests in isolated trees or edge situations (Orians and Kuhlman 1956, Bohm 1978). Mader (1978) suggested that red-tails do not use palo verde (*Cercidium* sp.) and ironwood trees (*Olneya tesota*) often as nest-sites because it is difficult for them to penetrate and construct nests in the dense canopy. Petersen (1979:20) felt that a free avenue of approach was an important factor in RTH nest-site selection. Titus and Mosher (1981) indicated that separating variables in their discriminant analysis of RSH and RTH nest-sites probably represented differences in accessibility. Considering the above, we hypothesize that given a suitable territory the overriding factor in Red-tailed Hawk tree nest-site selection is accessibility to the nest.

Red-shouldered Hawks have proportionately shorter wings and longer tails than RTH (Johnson and Peeters 1963:436), theoretically improving steering ability and maneuverability. Therefore, nest access probably is

TABLE 4

COMPARISON OF MEAN TREE DENSITY AND DBH DETERMINED BY THE QUADRAT AND POINT-QUARTER SAMPLING TECHNIQUES AT 12 RED-SHOULDERED AND 26 RED-TAILED HAWK NEST-SITES IN IOWA

Variable	Red-shouldered Hawk mean ± SD	Red-tailed Hawk mean ± SD	Probability[a]
Quadrat density (number of trees/ha)	643.0 ± 236.0	473.0 ± 216.0	0.0347*
Point density (number of trees/ha)	591.1 ± 193.0	393.0 ± 197.0	0.0065*
Quadrat dbh (cm)	21.5 ± 4.8	20.9 ± 6.4	0.7822
Point dbh (cm)	22.6 ± 4.3	22.7 ± 6.3	0.9641

[a] Student's *t*-test.
* Significant ($P < 0.05$).

less important, and red-shoulders are able to use nests lower in the canopy and with larger support branches, thereby protecting their young from insolation and adverse weather.

Nest-site vegetation.—Analysis of variance was used to test if differences in tree dbh or tree density existed among the seven points along the point-quarter transects extending from the nest-sites of each species. These analyses showed that tree dbh ($P > 0.1$) and tree density ($P > 0.1$) did not differ along the 64-m radii extending from the nest trees of either species.

The woodlots used by nesting RSH had greater tree densities than those used by nesting RTH (Table 4). This supports the hypothesis that RTH only used nest-sites with high accessibility. Selective cutting in dense woodlots could possibly open habitats currently used only by RSH to competition with RTH.

The mean dbh of trees around the nest-sites of both species were nearly identical (Table 4). However, Red-shouldered Hawks tended to nest in woodlots with more large canopy trees and fewer subcanopy ones than found in RTH nesting woodlots (Fig. 4). The difference was significant for quadrat data ($\chi^2 = 11.7$, df = 3, $P = 0.0086$), but not for the point-quarter data ($\chi^2 = 7.5$, df = 3, $P = 0.057$). Perhaps RSH, which commonly fly below the canopy (Bent 1937, Stewart 1943, Johnson and Peeters 1963, pers. obs.), selected woodlands with a larger proportion of canopy trees and thereby had fewer obstructions from small and middle-sized trees.

Mean tree density and dbh did not differ significantly ($P > 0.1$) between the two sampling techniques (Table 4). The point-quarter method tends to underestimate density when aggregated populations are sampled (Risser and Zedler 1968). Therefore, results from the quadrat method were used for the discriminant function analysis of nest-sites.

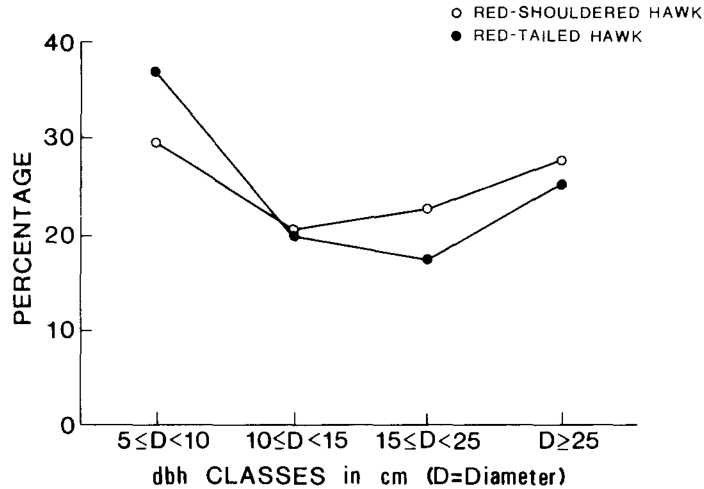

FIG. 4. Percentage of trees in four different dbh classes occurring within a 730-m^2 circular quadrat centered on 12 Red-shouldered and 26 Red-tailed hawk nests.

Nesting habitat.—For both species, hunting area was considered to be nonforested marsh, pasture, or other open area. Breeding RTH primarily hunt in nonforested areas (Smith and Murphy 1973, Howell et al. 1978, Petersen 1979:48). RSH also do much of their hunting in nonforested areas, primarily marshes and wet meadows (Craighead and Craighead 1956, Portnoy 1974, Bednarz 1979:71), although they may also hunt within woodlands.

RSH nesting habitat is characterized by a large area of floodplain forest, numerous small hunting areas, usually marshes and little cropland (Table 5). The large edge distance is an important indicator of this habitat. RTH nesting habitat is characterized by the presence of some upland forest, fewer but larger hunting areas, usually upland areas and a large area of cropland (Table 5).

Discriminant analysis correctly classified all 12 RSH nests and 24 of 26 RTH nests (Fig. 5). The most important variables in this discrimination, ranked according to their discriminant coefficient, were cropland area (1.03), upland forest area (0.88), number of feeding areas (0.63), upland hunting area (0.52) and edge distance (0.49).

Cropland area was by far the most important discriminating variable. As long as adequate hunting area (e.g., pastures) was available, the RTH was able to use agricultural lands. Large areas of cropland on level floodplains usually meant that marshes and forest habitats, important to RSH,

TABLE 5

COMPARISON OF 11 HABITAT PARAMETERS DETERMINED FROM A 1-KM RADIUS CIRCULAR PLOT CENTERED ON RED-SHOULDERED AND RED-TAILED HAWK NESTS IN IOWA

Variable	Red-shouldered Hawk mean ± SD (N = 12)	Red-tailed Hawk mean ± SD (N = 26)	Probability[a]
Floodplain forest (ha)	123.2 ± 75.6	11.3 ± 26.0	0.0003**
Upland forest (ha)	70.0 ± 51.7	92.5 ± 52.2	0.2244
Marsh (ha)	39.3 ± 22.9	5.0 ± 14.2	0.0002**
Upland nonforested hunting area (ha)	19.1 ± 17.4	70.5 ± 20.0	<0.0001**
Total nonforested hunting area (ha)[b]	58.4 ± 26.8	75.4 ± 24.1	0.578
Number of hunting areas	24.6 ± 12.1	14.0 ± 5.2	0.0124*
Mean size of hunting areas (ha)	2.8 ± 1.5	6.4 ± 4.0	0.0003**
Human use area (ha)	2.6 ± 4.2	4.5 ± 4.4	0.2099
Cropland (ha)	17.3 ± 17.1	113.2 ± 53.8	0.0001**
Open water (ha)	40.6 ± 20.5	11.3 ± 20.5	0.0002**
Edge (m)[c]	15,115.0 ± 6497.0	9718.0 ± 3990.0	0.0180*

[a] Student's t-test.
[b] Total hunting area includes marsh and upland hunting area.
[c] Edge is distance of forest bordering marsh or upland hunting areas.
* Significant ($P < 0.05$); ** significant ($P < 0.001$).

had been altered. Upland forest area probably was an important variable because it supplied hunting perches and, usually, the nesting area for RTH. Upland forest is probably not necessary for the Red-shouldered Hawk if adequate floodplain forest is available. RSH use of upland forest habitats in Iowa is primarily limited to peripheral areas immediately adjacent to floodplains (Bednarz and Dinsmore 1981). Both RTH and RSH will use and perhaps compete for floodplain forests of limited size, but RTH may avoid using floodplain forest that is surrounded by upland forest.

Upland hunting area was important in discrimination because it was found primarily in RTH habitats while marsh was the primary hunting area of RSH (Table 5).

Edge and number of feeding areas are important to RSH, which use numerous small marshes interspersed with forest (Bednarz and Dinsmore 1981). RTH seemed to prefer larger hunting areas with less interspersion and, hence, less edge (Table 5).

Nest habitat fell into three groups (Fig. 5). Outliers normally were the result of a single high or low value of one variable. The RSH group encircled by a solid line included three nests in a large floodplain forest (comprising 80% or more of the area) with no upland, agricultural land, or human development. Conversely, the RTH group of 20 nesting habitats consisted of a variety of cover types averaging 33% upland forest, 25%

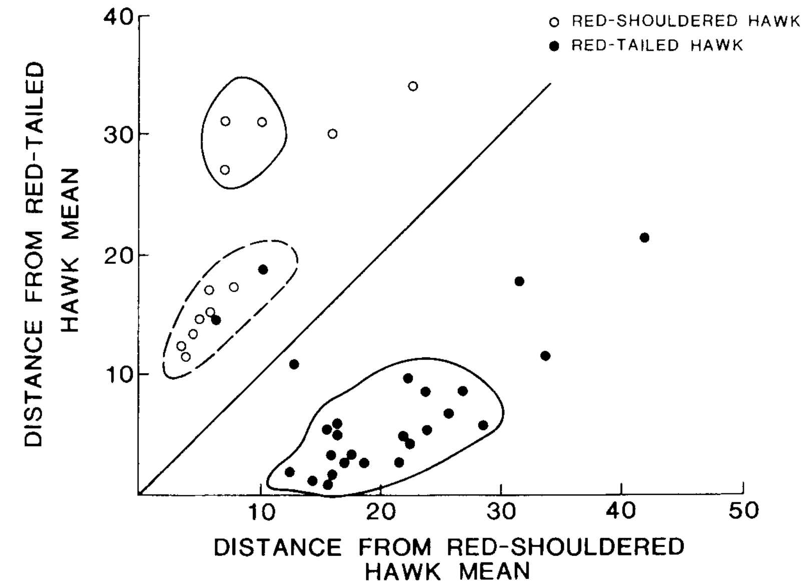

FIG. 5. Discriminant analysis of the habitat surrounding 12 Red-shouldered and 26 Red-tailed hawk nests represented by Mahalanobis distances from the respective means.

pasture or some type of hunting area, 35% cropland, and 7% other land uses, very similar to that described for Alberta (McInvaille and Keith 1974). The third group, within the dashed line, included seven RSH nests plus two RTH nests in floodplains. These habitats averaged 66% forest area (both bottomland and upland), but also included some area in cover types commonly identified with RTH (cropland, upland and human-use areas). This habitat could be considered a transition zone between typical red-shoulder and red-tail habitats which provide enough habitat for Red-shouldered Hawks that hunt within the floodplain forest and associated marsh and backwater areas. The two RTH pairs using this habitat were never seen hunting within the floodplain, but were seen flying to and from adjacent large, open hunting areas.

Nesting RSH generally are associated with extensive forest interspersed with small clearings or wet meadows (Bent 1937, Stewart 1949, Henny et al. 1973, Bednarz and Dinsmore 1981), while nesting RTH are found in open areas and are much less dependent on large woodlands (Fitch et al. 1946, Hagar 1957, Smith and Murphy 1973, Bock and Lepthien 1976, Howell et al. 1978).

Aggressive encounters between RSH and RTH have been reported (Dix-

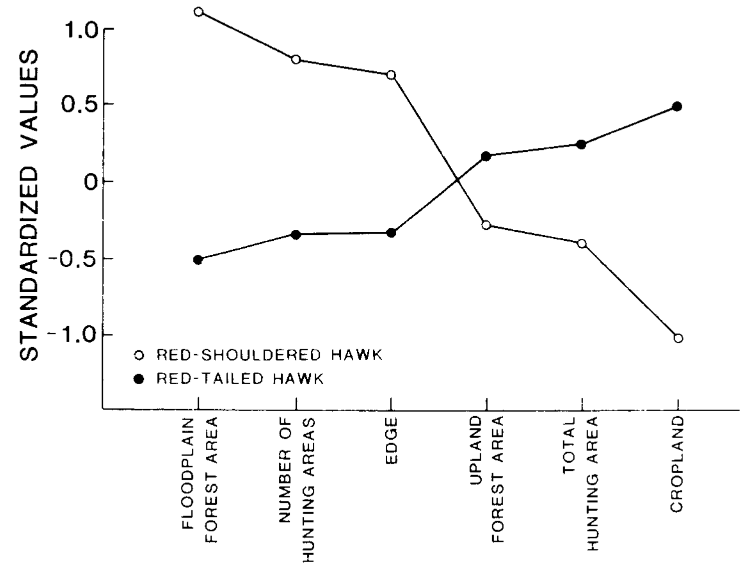

FIG. 6. Nesting habitat profiles of Red-shouldered and Red-tailed hawks in Iowa. Values were standardized by subtracting the mean and dividing by the standard deviation so that values between variables could be compared.

on 1928, Bent 1937, Kilham 1964, Portnoy 1974, Campbell 1975, pers. obs.). Austing (1964) noted that RSH and RTH alternately replaced each other in "fringe" areas. Craighead and Craighead (1956) suggested that RTH nested earlier in the year, and that the number of RSH that were able to nest was dependent on the number of RTH already established. In 6 years, they noted a loss of three RSH pairs and a gain of four RTH pairs occurring simultaneously with draining of swamps, cutting of woodlots and more intensive farming. These observations suggest that these two species compete for nesting areas. We suspect this competition probably is restricted to transitional habitat, and varies regionally. In Iowa, forest clearing and the development of pastures along drainage systems seems to have shifted the competitive advantage from RSH to RTH in bottomland areas. Additionally, the conversion of upland to intensive cultivation (i.e., corn and soybeans) has displaced the RTH and may have encouraged them to compete with RSH for altered habitats along river bottoms. Currently, RTH in Iowa nest extremely close to running water (Roosa 1964), while RSH are restricted to large wooded areas. We consider woodlands averaging 123 ha of floodplain forest and 70 ha of upland forest within 1 km of the nest (Table 5) a minimum size for the red-shoulder in Iowa.

Habitat profiles of six variables showed that Iowa RSH used a large area of floodplain forest, numerous small hunting areas and much edge, while RTH primarily used areas with upland forest along streams, relatively few large hunting areas and a large area of cropland (Fig. 6). A test for parallelism by using profile analysis (Morrison 1976) revealed highly significant differences between species ($F = 13.01$, $P < 0.0001$).

The RTH has been called an edge species (Bock and Lepthien 1976). However, our analysis demonstrates that the RSH occupies habitats with more edge than does the RTH (Table 5 and Fig. 6). The Iowa RTH probably is more accurately described as an openland species that requires perches.

The Red-shouldered Hawk in Iowa is a woodland species. The nest-site, vegetation analysis and nesting habitat all show that RSH typically used dense woodlands (Tables 1, 4, 5). As harvest of midwestern forests continues (Thomson 1980), the Red-shouldered Hawk undoubtedly will lose more of its optimum habitat, allowing competition and replacement by the larger Red-tailed Hawk.

SUMMARY

This study compares nest-site microhabitats and nesting habitats of Red-shouldered and Red-tailed hawks in northeastern and central Iowa. RSH and RTH nest-sites differed significantly in nest tree height; tree-nest height difference, nest tree dbh, canopy cover at nest height, mean support branch diameter, mean nest diameter, mean distance between support branches, slope of ground supporting nest tree, woodlot size, distance to nearest water, distance to nearest road and distance to nearest building. Red-tail nests were characterized by accessibility, being placed high in a tree, on small support branches, in areas of little canopy cover, typically on a hillside and having large distances between support branches. Red-shoulder nests usually had secure support and protection by being placed lower in trees, on large support branches, in areas of greater canopy cover, on level topography and having smaller distances between support branches. Red-shoulders built nests in woodlots with more canopy trees and a greater tree density than woodlots used by red-tails. The area of floodplain forest, marsh, upland nonforested hunting area, cropland, open water, number of hunting areas, mean size of hunting areas and total edge surrounding the nest differed significantly between species. Red-shoulders required large amounts of floodplain forest, edge and numerous small hunting areas. Red-tails typically were found in areas with nearly equal proportions of woodland, pasture and cropland. Logging in floodplain forests may open these areas to encroachment by red-tails and displacement of red-shoulders.

ACKNOWLEDGMENTS

Many individuals contributed to this study. We thank D. Roosa, D. Koenig and V. P. McCrow who provided encouragement, constructive advice and assistance in the field; R. Ervin, J. Wagner, M. Plouffe, P. Bartelt, J. McDonald, J. Schaufenbuel, G. Jones, F. Heinz, R. Renken, E. Johnson, M. Garrett and P. Knight also assisted in the field. R. Dahlgren coordinated the allocation of funding and assisted in other ways. D. Shenk, D. Cox and R. J. Harris assisted with the statistical analysis. K. Bildstein, H. Mueller, E. Klaas, D. Graham and M. Bachmann, reviewed this manuscript. Persons who provided suggestions or assistance in other ways include G. Ackerman, L. Best, B. Commings, B. Frederick, D. Hoffmaster, E. Martin, J. Mount, T. Munson, T. Nigus, B. Ohde, S. Postupalsky, M. Ryan, J. Schaefer, W. Smith, R. Sodja, D. Stauffer and G. A. Thibodeau. Funding was provided by the U.S. Fish and Wildlife Service (Migratory Birds Program) through the Iowa Cooperative Wildlife Research Unit (U.S. Fish and Wildlife Service, Iowa Conservation Commission, Iowa State University, and Wildlife Management Institute, cooperating), the Hawk Mountain Sanctuary Association, and the Iowa Agriculture and Home Economics Experiment Station. This is Journal Paper No. J-9612 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 2170.

LITERATURE CITED

AUSTING, G. R. 1964. The world of the Red-tailed Hawk. J.B. Lippincott Co., Philadelphia, Pennsylvania.

BARR, A. J., J. H. GOODNIGHT, J. P. SALL AND J. T. HELWIG. 1976. A user's guide to SAS 76. SAS Institute Inc., Raleigh, North Carolina.

BEDNARZ, J. C. 1979. I. Productivity, nest sites, and habitat of Red-shouldered and Red-tailed hawks in Iowa. II. Status, habitat utilization, and management of Red-shouldered Hawks in Iowa. M.S. thesis, Iowa State Univ., Ames, Iowa.

——— AND J. J. DINSMORE. 1981. Status, habitat utilization, and management of Red-shouldered Hawks in Iowa. J. Wildl. Manage. 45:236–241.

BENT, A. C. 1937. Life histories of North American birds of prey. Pt. 1. U.S. Natl. Mus. Bull. 167.

BOCK, C. E. AND L. W. LEPTHIEN. 1976. Geographical ecology of the common species of *Buteo* and *Parabuteo* wintering in North America. Condor 78:554–557.

BOHM, R. T. 1978. A study of nesting Red-tailed Hawks in central Minnesota. Loon 50:129–137.

CAMPBELL, C. A. 1975. Ecology and reproduction of Red-shouldered Hawks in the Waterloo region, southern Ontario. Raptor Res. 9:12–17.

CRAIGHEAD, J. J. AND F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania, and Wildlife Management Inst., Washington, D.C.

DIXON, J. B. 1928. Life history of the Red-bellied Hawk. Condor 30:228–236.

FITCH, H. S., F. SWENSON AND D. F. TILLOTSON. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48:205–237.

GATES, J. M. 1972. Red-tailed Hawk populations and ecology in east-central Wisconsin. Wilson Bull. 84:421–433.

GEIGER, R. 1965. The climate near the ground. Harvard Univ. Press. Cambridge, Massachusetts.

HAGAR, D. C., JR. 1957. Nesting populations of Red-tailed Hawks and horned owls in central New York State. Wilson Bull. 69:263–272.

HAHN, W., JR. 1927. Florida Red-shouldered Hawk. Oologist 44:141–142.

HENNY, C. J., F. C. SCHMID, E. M. MARTIN AND L. L. HOOD. 1973. Territorial behavior, pesticides, and the population ecology of Red-shouldered Hawks in central Maryland, 1943–1971. Ecology 54:545–554.

HOWELL, J., B. SMITH, J. B. HOLT, JR. AND D. R. OSBORNE. 1978. Habitat structure and productivity in Red-tailed Hawks. Bird-Banding 49:162–171.

JOHNSON, N. K. AND H. J. PEETERS. 1963. The systematic position of certain hawks in the genus *Buteo*. Auk 80:417–446.

JOHNSON, S. J. 1975. Productivity of the Red-tailed Hawk in southwestern Montana. Auk 92:732–736.

KILHAM, L. 1964. Interspecific relations of crows and Red-shouldered Hawks in mobbing behavior. Condor 66:247–248.

LUTTICH, S. N., L. B. KEITH AND J. D. STEPHENSON. 1971. Population dynamics of the Red-tailed Hawk (*Buteo jamaicensis*) at Rochester, Alberta. Auk 88:75–87.

MADER, W. J. 1978. A comparative nesting study of Red-tailed Hawks and Harris' Hawks in southern Arizona. Auk 95:327–337.

MCINVAILLE, W. B., JR. AND L. B. KEITH. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. Can. Field-Nat. 88:1–20.

MORRISON, D. F. 1976. Multivariate statistical methods. 2nd ed. McGraw-Hill Book Co., New York, New York.

MOSHER, J. A. AND C. M. WHITE. 1976. Directional exposure of Golden Eagle nests. Can. Field-Nat. 90:356–359.

MUELLER-DOMBOIS, D. AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York, New York.

ORIANS, G. AND F. KUHLMAN. 1956. Red-tailed Hawk and horned owl populations in Wisconsin. Condor 58:371–385.

PETERSEN, L. 1979. Ecology of Great Horned Owls and Red-tailed Hawks in southeastern Wisconsin. Wisconsin Dept. Nat. Resour. Tech. Bull. 111.

PORTNOY, J. W. 1974. Some ecological and behavioral aspects of a nesting population of Red-shouldered Hawks (*Buteo lineatus lineatus*). M.S. thesis, Univ. Massachusetts, Amherst, Massachusetts.

——— AND W. E. DODGE. 1979. Red-shouldered Hawk nesting ecology and behavior. Wilson Bull. 91:104–117.

RISSER, P. G. AND P. H. ZEDLER. 1968. An evaluation of the grassland quarter method. Ecology 49:1006–1009.

ROOSA, D. M. 1964. Nesting of raptors in western Wright County. Iowa Bird Life 34:88–90.

SEIDENSTICKER, J. C., IV, AND V. REYNOLDS, III. 1971. The nesting, reproductive performance and chlorinated hydrocarbon residues in the Red-tailed Hawk and Great Horned Owl in south-central Montana. Wilson Bull. 83:408–418.

SMITH, D. G. AND J. R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 18(3):1–76.

SNEDECOR, G. W. AND W. G. COCHRAN. 1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, Iowa.

STEWART, C. A. 1943. Nesting of the Red-shouldered Hawk in Sarpy County. Nebraska Bird Rev. 11:25–30.

STEWART, R. E. 1949. Ecology of a nesting Red-shouldered Hawk population. Wilson Bull. 61:26–35.

THOMSON, G. W. 1980. Iowa's disappearing woodlands. Iowa State J. Res. 55:127–140.

TITUS, K. AND J. A. MOSHER. 1981. Nest-site habitat selected by woodland hawks in the central Appalachians. Auk 98:270–281.

WILEY, J. W. 1975. The nesting habitat and reproductive success of Red-tailed Hawks and Red-shouldered Hawks in Orange County, California, 1973. Condor 77:133–139.

DEPT. ANIMAL ECOLOGY, IOWA STATE UNIV., AMES, IOWA 50011. (PRESENT ADDRESS JCB: 3832 GOODRICH NE, ALBUQUERQUE, NEW MEXICO 87110.) ACCEPTED 20 APR. 1981.