HABITAT CHARACTERISTICS OF GREAT HORNED OWLS IN SOUTHCENTRAL PENNSYLVANIA

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ABSTRACT.—We compared habitat characteristics associated with high- and low-use areas of great horned owls (*Bubo virginianus*) in forest, farm, and mixed forest-farm habitats in southcentral Pennsylvania during 1987 and 1988. High-use areas in forest habitats had a lower number (P < 0.05) of land-use cover types and a lower percent of deciduous forest cover than low-use areas. In farm habitats, high-use areas were significantly (P < 0.05) lower in elevation than low-use areas. In mixed habitats, high-use areas had a greater (P < 0.05) percent of cropland and pasture and lower percent of both deciduous and total forest cover than low-use areas. The overall correct classification rate in distinguishing between high- and low-use areas using stepwise logistic regression was relatively low. Stepwise logistic regression was not useful in predicting habitat characteristics important to great horned owls in each of the three habitats. Great horned owls in Pennsylvania are habitat generalists but tend to be associated with fragmented landscapes that contain nesting and foraging sites.

KEY WORDS: Bubo virginianus; farm habitat; forest habitat; great horned owl; habitat characteristics.

Características del hábitat de Bubo virginianus en el centro-sur de Pennsylvania

RESUMEN.—Comparamos características del hábitat de *Bubo virginianus* asociadas a usos alto y bajos, en bosques, áreas de cultivo y situaciones mixtas del centro-sur de Pennsylvania entre 1987 y 1988. Hábitat de bosques con áreas de alto uso tenían menor cobertura (P < 0.05) de otros tipos de hábitat y además tenían un porcentaje de cobertura de bosque deciduo menor que en áreas de bajo uso. En hábitat agrícolas, áreas de alto uso fueron significativamente más bajas (P < 0.05) en elevación que en áreas de bajo uso. En hábitat agrícolas, áreas de alto uso fueron significativamente más bajas (P < 0.05) en elevación que en áreas de bajo uso. En hábitat agrícolas, áreas de alto uso tenían un gran porcentaje (P < 0.05) de cultivos y pasturas y un porcentaje de cobertura tanto de bosque deciduo como del bosque en su totalidad menor que en áreas de bajo uso. La distinción entre áreas de alto y bajo uso, usando una regresión logística paso a paso, fue relativamente baja. Este método estadístico no fue útil en predecir características de hábitat importantes para *B. virginianus*, en cada uno de los tres hábitat estudiados. *B. virginianus* en Pennsylvania hábitat-generalistas, pero tienden a estar asociados con paisajes fragmentados que contienen sitios de nidificación y forrajeo.

[Traducción de Ivan Lazo]

Populations of great horned owls (*Bubo virgini*anus) have increased in some areas of Pennsylvania since the early 1970s (Goodrich and Senner 1989), but habitat use by great horned owls in Pennsylvania is poorly understood (Morrell and Yahner 1990). A better knowledge of habitat use by these owls, however, is vital to determine the influence of current and future land-use practices on population trends of this species. Land-use practices that create openings in heavily forested areas may contribute to increased numbers of great horned owls in Pennsylvania by providing foraging habitat for owls and suitable habitat for prey species (Goodrich and Senner 1989). Our objective was to compare habitat characteristics of areas receiving high and low use by great horned owls in forest, farm, and mixed forest-farm habitats of southcentral Pennsylvania.

Methods

We conducted surveys of great horned owls along 56 16-km routes in 15 counties of southcentral Pennsylvania from early January to late May, 1987 and 1988. To select routes, 30 of 126 topographic maps (1:24 000) covering the study area were randomly selected. Two 16-km routes then were established on each map by randomly choosing a light-duty road from the map. Direction of travel along a route was selected randomly. If a route occurred within 1.6-km of another route or if it meandered excessively, it was modified or excluded to avoid covering an area more than once.

Ten stations were established at 1.6-km intervals along each survey route. Owls were surveyed by broadcasting a tape recording of the call of a "hooting" great horned owl

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Table 1. Abbreviations and description of 16 habitat characteristics used in analyses of habitat use by great horned owls in south-central Pennsylvania from January to May 1987 and 1988. Characteristics were measured within a 0 8-km radius circular plot centered on each survey station and taken from USGS 7.5-min topographic maps and aerial photographs (1:10 000).

Abbreviation	DESCRIPTION
COVTYPE	Number of different land-use cover types (characteristics RESID to ORCHARD below are taken from Anderson et al. [1976], see Appendix 1 for detailed descriptions of the cover types).
PATCHES	Number of individual patches of land-use cover types, where patches are defined as individual areas of a specific land-use cover type regardless of patch size that can be delineated on the aerial photographs.
INTRSPR	Index of habitat interspersion (Baxter and Wolfe 1972).
ELEV	Elevation (m) at center of the plot.
RUGGED	Index of terrain ruggedness (Beasom et al. 1983).
RESID	Percent of residential cover.
URBAN	Percent of urban cover (includes all other built-up areas other than residential).
WATER	Percent of reservoir and lake cover.
ROAD	Percent of paved road cover.
AGRIC	Percent of cropland and pasture cover.
DECID	Percent of deciduous forest cover.
CONIF	Percent of coniferous forest cover.
MIXED	Percent of mixed (combination of DECID and CONIF) forest cover.
TOTFOR	Percent of total forest cover.
RIPAR	Percent of wetland/riparian cover (includes marshes, wet meadows, streams, and rivers).
ORCHARD	Percent of orchard, grove, and vineyard cover.

(hereafter referred to as a broadcast) obtained from the Cornell Library of Natural Sounds, using a speaker-amplifier system (Perma-Power Half-Miler Hailer, Model S-610) and a portable cassette player (Realistic CTR-71). The system consisted of an 8-ohm speaker and a 40-watt amplifier. At each station, an observer exited the vehicle and listened for unsolicited owl calls (a "hooting" owl) for 2 min. The broadcast then was played for 5 min and 20 sec, during which all responding owls were recorded. A broadcast consisted of six sets of a 20-sec owl call, with each set separated by a 40-sec pause. Each set consisted of a series of four to seven note songs. The first 20-sec broadcast was made holding the speaker perpendicular to the road, with the speaker rotated 180° following each 20sec broadcast. Immediately after the final 20-sec broadcast, 5 min were spent at the station to record locations of responding owls on a topographic map. Audio output of the playback was adjusted periodically to maintain 90-110 decibels (Fuller and Mosher 1987) as recorded by a hand-held sound meter. All surveys were conducted between 1600 and 0800 H. Surveys were not conducted when wind velocity consistently exceeded 12 km/hr (as measured with a hand-held anemometer) or when precipitation was steady.

Each survey station was classified into one of three habitats using aerial photographs (black and white, 1:10 000 scale): forest, farm, or mixed. Classification was based on vegetative and land-use cover characteristics within a 0.8-km radius circular plot centered on each survey station. When $\geq 67\%$ of the area within the radius was in forest cover, we classified the station as forest habitat. Similarly,

if $\geq 67\%$ of the area was agricultural land, the survey station was classified as farm habitat. Forest and agricultural cover were based on definitions provided by Anderson et al. (1976). When cover characteristics at a survey station did not fall into either of the above categories, it was designated mixed (forest-farm) habitat.

We used an 0.8-km radius because a vocalization of a great horned owl can be heard from a distance of up to 1 km (Rusch 1982). Thus, all owls vocalizing within the 0.8-km radius circle probably were detected. In addition, many researchers have reported that the majority of activity by great horned owls during their breeding season is confined to an area less than 0.8-km of their nest (Baumgartner 1939, Craighead and Craighead 1959, Fuller 1979, Petersen 1979). Although there may have been instances when a territory did overlap two plots, a single sample plot was sufficiently large in most cases to encompass all or most of a given territory.

We quantified 16 habitat characteristics along 34 survey routes randomly selected from the 56 survey routes (Table 1). Habitat characteristics within each 0.8-km radius were taken from aerial photographs or U.S. Geological Survey 7.5-min topographic maps and included 11 land-use cover types, two topographic features, and three measures of habitat heterogeneity. We measured each characteristic within the 0.8-km radius circular plot.

Percent of each land-use cover type (Level II, Anderson et al. 1976; Appendix 1) within a plot was determined using a Calcomp 9100 digitizer and Earth Resources Data Analysis Systems (program "Measure"). Two measures of topographic features, elevation (ELEV) and ruggedness (RUGGED; Beasom et al. 1983), were obtained from topographic maps. Elevation (m) was recorded at the center of each 0.8-km radius circular plot. RUGGED was determined using an acetate overlay, which consisted of a uniform grid of 98 dots within the 0.8-km radius plot. The number of intersections of dots and contour lines was counted, and RUGGED was calculated as the ratio of dot-contour intersections to total number of dots (N = 98) in the grid.

Three measures of landscape heterogeneity used were the number of different land-use cover types (COV-TYPE), number of individual patches of land-use cover type (PATCHES), and an interspersion index (INTRSPR). The number of individual patches was recorded by counting the number of patches regardless of cover type or size. We used a modified version of the Baxter-Wolfe method to obtain an interspersion index (Baxter and Wolfe 1972, Hall 1984).

The area defined within the 0.8-km radius circular plot was classified as either a high- or a low-use area by great horned owls. A high-use area was designated if two or more owl contacts occurred at the station based on the total visits combined (N = 3-7) to that station in a field season. A low-use area was designated if less than two owl contacts were noted during the total visits. Robbins (1970) recommended that two or more contacts of a singing bird recorded in seven visits to an area provided significant evidence for determining the presence of a breeding territory.

Habitat characteristics were compared between highand low-use areas using single-classification analysis-ofvariance and Mann-Whitney rank sums tests (Sokal and Rohlf 1981). Characteristics were compared between highand low-use areas based on all stations combined and between high- and low-use areas based on stations in forest, farm, and mixed habitat considered separately. Normality of each characteristic was tested using the Kolomogrov D statistic and normal probability plots (SAS 1985). To test the assumption of homogeneity of variances, the folded form of the F statistic, F', was used (SAS 1985).

Stepwise logistic regression (Dixon 1985) was used to determine which habitat characteristics best distinguished between high- and low-use areas for all stations combined and for each habitat category separately. The asymptotic covariance estimation was used to calculate F-values for entry and removal of characteristics from the models. Associated P-values for entry and removal of characteristics were 0.10 and 0.15, respectively. A characteristic was used in the regression model if comparisons between high- and low-use areas produced an F-statistic of P < 0.10. To reduce redundancy with other characteristics, only one pair of highly correlated (P < 0.05) characteristics was used in the model. However, we retained DECID for the farm habitat model because DECID was significant in segregating between high- and low-use areas in the final logistic regression models for both forest and mixed habitats.

We developed three regression models for all stations combined and for each habitat category (i.e., forest, farm, mixed). One model was developed using continuous characteristics, and two other models were developed using categorical characteristics. Two categorical models used variables DECID and AGRIC arbitrarily separated into five (≤ 20 , 21-40, 41-60, 61-80, and $\geq 81\%$ cover) and three categories (≤ 33 , 34-66, and $\geq 67\%$ cover, respectively). Other characteristics arbitrarily separated into interval categories where ELEV (≤ 150 , 151-300, 301-450, and ≥ 451 m), RIPAR (≤ 20 and $\geq 21\%$ cover), and RUG-GED (≤ 20 , 21-40, 41-60, ≥ 61) after examining the distribution of the continuous values.

RESULTS

We classified 134 (39%) and 206 (61%) of the survey stations as high- and low-use areas, respectively. One-hundred twenty-six (37%) of the 340 stations were classified as forest, 79 (23%) as farm, and 135 (39%) as mixed habitats. Fifty-nine percent of the stations in farm habitat, 43% in mixed habitat, and 23% in forest habitat were considered high-use areas.

High-use areas, based on all habitats combined, were lower in elevation (ELEV), had a greater percent of cropland and pasture cover (AGRIC), and lower percentage of both deciduous forest (DECID) and total forest cover (TOTFOR) compared to lowuse areas (Table 2).

In forest habitats, high-use areas had a lower number of different land-use cover types (COV-TYPE) and a lower percent of deciduous forest cover (DECID) than low-use areas (Table 2). In farm habitats, high-use areas were significantly lower in elevation (ELEV) than low-use areas. In mixed habitats, high-use areas had a greater percent of AGRIC and lower percent of both DECID and total forest cover (TOTFOR) than low-use areas.

Only three characteristics were used in the stepwise regressions for all habitats combined, and two entered the final models (Table 3). DECID and ELEV contributed significantly to the improvement of each model, but the model that used continuous characteristics provided a poor fit. The model using five categories for DECID provided the best overall correct classification.

Three characteristics also were used in the forest habitat models, but only DECID and COVTYPE were retained in the final models (Table 3). Both characteristics significantly improved the fit of the model and also improved the overall fit. The model using five categories for DECID provided the best overall fit.

Two characteristics were used in the stepwise logistic regression of farm habitat, and only ELEV entered into each of the final models (Table 3). ELEV significantly improved each model, but the overall

				НЛ	BITAT			
HABITAT	Ţ	OTAL	FOI	REST	F	ARM	IM	XED
CHARAC- TERISTIC	High-use Area	Low-use Area	High-use Area	Low-use Area	HIGH-USE Area	Low-use Area	High-use Area	Low use Area
COVTYPE ^a	3.5 ± 0.1	3.6 ± 0.1	3.1 ± 0.1	3.6 ± 0.1^{c}	3.4 ± 0.2	3.1 ± 0.1	3.8 ± 0.1	3.8 ± 0.1
PATCHES ^a	10.0 ± 0.4	9.8 ± 0.3	8.6 ± 0.8	9.1 ± 0.6	8.9 ± 0.6	9.1 ± 0.8	11.7 ± 0.6	11.1 ± 0.6
INTRSPR^a	9.1 ± 0.3	8.9 ± 0.3	7.5 ± 0.7	8.1 ± 0.5	7.5 ± 0.6	7.7 ± 0.8	11.1 ± 0.5	10.4 ± 0.6
ELEVa	285.5 ± 10.3	$344.0 \pm 9.9^{\circ}$	377.9 ± 20.3	384.1 ± 13.7	211.9 ± 12.2	$266.3 \pm 25.2^{\circ}$	299.0 ± 14.8	325.8 ± 15.7
RUGGED ^a	22.7 ± 1.3	26.3 ± 1.2	28.3 ± 3.3	29.4 ± 1.9	16.0 ± 1.7	17.9 ± 2.4	25.3 ± 2.0	25.4 ± 1.9
RESID ^b	0.3 ± 0.1	0.7 ± 0.2	0.3 ± 0.2	0.5 ± 0.2	0.3 ± 0.2	I	0.5 ± 0.3	1.3 ± 0.5
URBAN ^b	0.07 ± 0.01	0.06 ± 0.02	1	0.1 ± 0.1	0.2 ± 0.1	I	1	0.03 ± 0.03
LAKE ^b	0.3 ± 0.2	0.3 ± 0.1	0.03 ± 0.04	0.3 ± 0.2	0.02 ± 0.02	0.1 ± 0.1	0.6 ± 0.5	0.3 ± 0.3
ROADS ^b	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	0.7 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.4 ± 0.08
AGRIC ^a	53.6 ± 2.2	$36.5 \pm 1.8^{\circ}$	19.5 ± 3.3	17.2 ± 1.6	80.5 ± 1.3	79.1 ± 2.2	48.4 ± 1.2	$43.2 \pm 1.4^{\circ}$
DECID ^a	23.6 ± 1.9	$40.4 \pm 1.9^{\circ}$	43.7 ± 5.6	57.4 ± 2.7^{c}	10.4 ± 1.2	10.0 ± 1.7	24.3 ± 2.5	$31.5 \pm 2.2^{\circ}$
CONIF ^b	3.7 ± 0.5	3.6 ± 0.4	6.5 ± 1.6	4.1 ± 0.6	1.0 ± 0.2	1.3 ± 0.5	4.3 ± 0.7	3.9 ± 0.7
MIXED ^a	16.9 ± 1.7	16.6 ± 1.3	28.3 ± 5.8	19.1 ± 2.2	7.0 ± 1.1	8.8 ± 1.6	19.3 ± 2.3	16.7 ± 2.0
TOTFOR ^a	44.1 ± 2.2	60.5 ± 1.7^{c}	78.4 ± 3.2	80.5 ± 1.5	18.4 ± 1.4	20.2 ± 2.2	47.9 ± 1.5	52.1 ± 1.5
RIPAR ^a	0.7 ± 0.2	0.6 ± 0.2	0.03 ± 0.0	0.3 ± 0.1	0.4 ± 0.2	0.1 ± 0.1	1.2 ± 0.6	1.2 ± 0.5
ORCHARD ^a	0.3 ± 0.2	0.5 ± 0.2	1.0 ± 1.0	0.2 ± 0.1	0.04 ± 0.04	0.1 ± 0.1	0.1 ± 0.1	1.1 ± 0.6
^a Tested with Stur ^b Tested with Mar	dent's <i>t</i> -test. nn-Whitney rank si	im test						
^c Significant differ	ence $(P \le 0.05)$ bet	tween high-use and lo	w-use areas within a	given habitat.				

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Table 2. Mean (\pm SE) of 16 habitat characteristics measured at high- and low-use areas (N = 340) of great horned owls in three habitats in south-central Pennsylvania from January to May, 1987 and 1988. Units for habitat characteristics are given in text.

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	Coeffi- cient	SE of Coeffi- cient	Improvement Chi-square		Goodness-of-fit Chi-square		Percent Correct Classification	
Habitat			x ²	P-value	x ²	P-VALUE	HIGH-USE	Low-use
All habitats ^a								
DECID	0.509	0.0106	34.0	0.000	62.9	0.087	66.2	67.6
ELEV	0.362	0.0148	6.2	0.013	56.8	0.180		
Constant	-1.572							
Forest ^a								
DECID	0.425	0.166	5.1	0.024	25.3	0.280	35.7	87.5
COVTYPE	0.449	0.201	5.2	0.022	20.1	0.514		
Constant	-1.572							
Farm ^b								
ELEV	0.684	0.351	4.2	0.04	7.6	0.176	93.6	25.0
Constant	-1.841							
Mixed ^a								
DECID	0.505	0.208	6.1	0.013	8.7	0.463	50.0	69.7
Constant	-0.702							

Table 3. Stepwise regression models for distinguishing habitat characteristics between high- and low-use areas of great horned owls in south-central Pennsylvania from January to May 1987 and 1988. Models were based on 133 high-use and 206 low-use areas in forest, farm, and mixed forest/farm habitats.

^a Model used categorical characteristics: DECID (≤ 20 , 21-40, 41-60, 61-80, and $\geq 81\%$), ELEV (≤ 150 , 151-300, 301-450, and ≥ 451 m), and RUGGED (≤ 20 , 21-40, 41-60, ≥ 61).

^b Model used categorical characteristics: DECID (\leq 33, 34–66, and \geq 67%), ELEV (\leq 150, 151–300, 301–450, and \geq 451 m), and RUGGED (\leq 20, 21–40, 41–60, and \geq 61).

fit was generally poor except for the model that used three categories for DECID. All models for farm habitat provided the same overall correct classification.

Two variables were used in the final model for mixed habitat (Table 3). AGRIC entered into the final model that used continuous characteristics, and DECID entered into the final model that used five categories for DECID and AGRIC. No characteristic was significant in distinguishing between highand low-use areas in the model that used three categories for DECID and AGRIC. DECID significantly improved the fit of the categorical model and also provided a relatively good overall fit.

We found no significant change in any models when the variable DECID was replaced with TOT-FOR. A high correlation was found between DE-CID and TOTFOR (r = 0.71, df = 338, P = 0.0001).

DISCUSSION

We did not identify habitat characteristics that were common to areas receiving high and low use in farm, forest, and mixed forest-farm habitats in southcentral Pennsylvania. High-use areas, how-

ever, had greater amounts of open cropland and pasture cover and lower amounts of deciduous and total forest cover than low-use areas, which generally was consistent with other studies. In Virginia, McGarigal and Fraser (1984) reported that great horned owls preferred old forest stands (>80 vr old) adjacent to farmlands. In Minnesota (Fuller 1979) and Wisconsin (Petersen 1979), agricultural and undisturbed fields comprised a larger proportion of the home range of great horned owls than other habitat types because owls used fields and forest edges while foraging. Furthermore, Fuller (1979) and Petersen (1979) found that radio-tagged owls used forested habitat proportionately more often than expected based on its availability even though forested habitat comprised a relatively small proportion of the home range of an owl. Fuller (1979) cautioned that low use of a habitat, as determined by radiotelemetry, may be biologically misleading. Owls, for example, may be using an important habitat, such as an agricultural field, only to forage for prey before returning for longer periods to a different habitat, such as a woodlot containing a nest with young.

In this study, forest cover predominated on upland

ridges and agriculture was common to valleys. Thus, high-use areas were at lower elevations characterized by abundant fields and forest edges. This was especially noticeable in farm habitat where owls were often found in small woodlots along drainages and stream bottoms, which were areas lower in elevation than upland areas used for agricultural purposes. However, elsewhere agricultural areas can occur at higher elevations than forested areas (e.g., Allegheny Plateau physiographic region). Additional research is needed to determine if high-use areas in other regions are a function of the extent of farm habitat or simply due to elevational differences.

A reduced amount of deciduous forest cover in high-use than in low-use areas in both forest and mixed habitats in our study suggests that this landscape feature is important in determining habitat use by great horned owls in Pennsylvania. Petersen (1979) found that successful males (those producing >1 fledgling) used woodlots less frequently than unsuccessful males. He reasoned that a successful male spent more time in non-forested areas, such as lowland pastures and strip cover, to feed its mate and nestlings.

No difference was found in the amount of forest cover between high- and low-use areas in farm habitat, perhaps because foraging areas in farm habitats were plentiful. Thus, habitat suitability for great horned owls in farm habitat may be limited by other factors, such as the availability of adequate nesting and roosting sites. McInvaille and Keith (1974) and Baumgartner (1939) suggested that habitat suitability for great horned owls may depend on number and proximity of open non-forested areas. Craighead and Craighead (1959) reported that the distribution of suitable woodlots (>4.0 ha) determined the distribution and density of great horned owls in Wisconsin and all woodlots containing nesting owls had extensive proximal non-forested uncultivated land.

One possible explanation why few habitat characteristics distinguished between high- from low-use areas is that great horned owls may select territories based on characteristics not measured in our study. For example, we did not quantify prey densities and distribution, but these may be important to habitat selection by some owls (Adamcik et al. 1978). Moreover, perhaps methods used in our study to measure habitat characteristics may not provide an accurate assessment of the habitat or were not precise enough to show differences in habitats that great horned owls perceive as being biologically important.

In summary, we conclude that great horned owls in Pennsylvania are habitat generalists. Factors influencing habitat use by great horned owls may simply be a suitable nesting site that is adjacent to open non-forested areas used for foraging. We recommend that other studies evaluate characteristics of great horned owls on a smaller sampling area (e.g., 0.4km radius) than that used in our study. Perhaps a smaller sampling area would provide a better indication of habitat use by an owl because a larger sampling area increases the possibility of including non-use areas within a high-use survey plot. In addition, non-significant characteristics that occurred infrequently in our study (e.g., urban, roads, orchard) should be eliminated from consideration as important owl habitat characteristics in future studies

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LITERATURE CITED

- ADAMCIK, R.S., A.W. TODD AND L.B. LLOYD. 1978. Demographic and dietary responses of great horned owls during a snowshoe hare cycle. Can. Field-Nat. 9: 156-166.
- ANDERSON, J.R., E.E. HARDY, J.T. ROACH AND R.E. WITMER. 1976. A land use and land cover classification system for use with remote sensor data. U.S Geol. Surv. Prof. Pap. 964. Washington, DC U.S.A
- BAUMGARTNER, F.M. 1939. Territory and population in the great horned owl. Auk 56:274-282.
- BAXTER, W.L. AND C.W. WOLFE. 1972. The interdispersion index as a technique for evaluation of bobwhite quail habitat. Pages 158-165 in J.A. Morrison and J.C. Lewis [EDS.], Trans. First Quail Symp. Oklahoma State Univ., Stillwater, OK U.S.A.
- BEASOM, S.L., E.P. WIGGERS AND J.R. GIARDINO. 1983 A technique for assessing land surface ruggedness. J Wildl. Manage. 47:1163-1166.
- CRAIGHEAD, J.J. AND F.C. CRAIGHEAD. 1959. Hawks, owls, and wildlife. Stackpole, Harrisburg, PA U.S.A.

- DIXON, W.J. [ED.]. 1985. BMDP statistical software. Univ. California Press, Berkeley, CA U.S.A.
- FULLER, M.R. 1979. Spatiotemporal ecology of four sympatric raptor species. Ph.D. dissertation. Univ. Minnesota, Minneapolis, MN U.S.A.
- AND J.A. MOSHER. 1987. Raptor survey techniques. Pages 37-65 in B.A. Giron Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.], Raptor management techniques manual. Natl. Wildl. Fed., Washington, DC U.S.A.
- GOODRICH, L.J. AND S.E. SENNER. 1989. Recent trends of wintering great horned owls (*Bubo virginianus*), redtailed hawks (*Buteo jamaicensis*) and two of their avian prey in Pennsylvania. J. Pa. Acad. Sci. 62:131-137.
- HALL, P.A. 1984. Characterization of nesting habitat of goshawks (Accipiter gentilis) in northwestern California. M.S. thesis, Humboldt State Univ., Arcata, CA U.S.A.
- McGARIGAL, K. AND J.D. FRASER. 1984. The effects of forest stand age on owl distribution in southwestern Virginia. J. Wildl. Manage. 48:1393-1398.
- MCINVAILLE, W.B. AND L.B. KEITH. 1974. Predatorprey relations and breeding biology of great horned

owls and red-tailed hawks in central Alberta. Can. Field-Nat. 88:1-20.

- MORRELL, T.E. AND R.H. YAHNER. 1990. Status and habitat characteristics of the great horned owl in Pennsylvania. Final Rep., School of Forest Resources, Pennsylvania State Univ., University Park, PA U.S.A.
- PETERSEN, L. 1979. Ecology of great horned owls and red-tailed hawks in southeastern Wisconsin. Wisconsin Dept. Nat. Resour. Tech. Bull. No. 111. Madison, WI U.S.A.
- ROBBINS, C.S. 1970. Recommendations for an international standard for a mapping method in bird census work. Audubon Field Notes. 24:723-726.
- RUSCH, D.H. 1982. Great horned owl. Pages 87-88 in D.E. Davis [ED.], CRC handbook of census methods for terrestrial vertebrates. CRC Press Inc., Boca Raton, FL U.S.A.
- SAS INSTITUTE INC. 1985. SAS User's guide: statistics, version 5 edition. Cary, NC U.S.A.
- SOKAL, R.R., AND F.J. ROHLF. 1981. Biometry. W.H. Freeman, San Francisco, CA U.S.A.

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Appendix 1. Definitions of characteristics used to define land-use cover types in south-central Pennsylvania, 1987 and 1988. Definitions are modified Level-II classifications (Anderson et al. 1976).

Characteristic	DEFINITION					
RESID	Areas of occupied dwellings ranging from high-density (multiple-unit structures of urban cores) to low-density (houses are on lots of more than an 0.4 ha on the periphery of urban expansion). Linear residential developments along transportation routes are included.					
URBAN	Includes all other built-up areas of intensive use, including towns, cities, strip developments, shopping and industrial centers, mills, institutions, commercial complexes, mining opera- tions, cemeteries, waste dumps, ski areas, railroad transportation routes, airports, quarries, strip mines, and all areas of open land that are intensively used, such as parks and golf courses. Included in the above definition are some characteristics defined as Other Urban or Built-up Land by Anderson et al. (1976).					
ROAD	All paved roads that are two lanes or wider.					
CROP	All land used primarily for the purposes of cropland and pasture.					
ORCHARD	Includes orchards, groves, and vineyards. Tree nurseries and plantations were included in this cover type in our study.					
WATER	Bodies of water that, if linear, are at least 0.20-km wide and, if extended, cover at least 16 ha or areas of water that are non-flowing, naturally enclosed bodies of water (including islands too small to delineate), and artificial impoundments of water used for irrigation, recreation, hydroelectric power generation. Lakes and reservoirs are classified separately by Anderson et al. (1976), but as one cover type for our study.					
DECID	All forested areas having a predominance of trees (i.e., $>67\%$) that lose leaves at the end of the frost-free season or at the beginning of the dry season.					
CONIF	All forested areas having a predominance of trees (i.e., $>67\%$) that remain green throughout the year.					
MIXED	All forested areas having an intermixture (33–67%) of both coniferous and deciduous trees.					
RIPAR	Includes wet meadows, bogs, or swamps, and seasonally wet or flooded basins, playas, or pot- holes with no surface-water outflow. Also included are streams and rivers where the water course is uninterrupted by a control structure. Riparian includes streams and rivers as de- fined by Anderson et al. (1976), who defines each separately.					