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Influence of nest cover on habitat selection in Clay-colored Sparrows.—Prevailing hypotheses (Rosenzweig 1981, 1985; Conner et al. 1986) contend that feeding opportunity is the primary influence on habitat selection in birds. Feeding opportunity may indeed determine habitat selection for many bird species because birds, in general, must feed themselves

and their young on food available within their territories. Clay-colored Sparrows, however, forage only outside their breeding territories (Knapton 1979, 1980). They stake their unusually small (1000 m²) territories in dense stands of low shrubs and fly to distant grasslands or cultivated fields to forage (Knapton 1979). Thus, the prevailing hypotheses on habitat selection apparently do not apply to Clay-colored Sparrows. Nonetheless, in the absence of foraging pressures, territorial Clay-colored Sparrows still prefer certain habitat features and avoid others (Walkinshaw 1939, Knapton 1979). In Manitoba, for example, Knapton (1979) observed that the low shrub *Symphoricarpos occidentalis* dominated vegetation within territories; he identified this shrub as a limiting resource because territory size and shrub density were negatively correlated.

Martin and Roper (1988) proposed an alternative hypothesis that the main determinant of habitat selection for some bird species is nest cover. Indeed, high quality nest cover can improve the territory-holder's fitness by reducing both nest predation (Yahner and Cypher 1986, Martin and Roper 1988) and mortality of nestlings due to harsh weather (Calder 1973, Walsberg 1981). If nest cover determines habitat selection in Clay-colored Sparrows, then the habitat features males include in their territories should have high value as nest cover relative to available habitat features. I tested this prediction by comparing vegetation within and outside the territories.

Study area and methods. — The study area was part of a 226-km² grassland in Buena Vista Township, Portage County, central Wisconsin (44°17'N, 89°34'W). Before being drained, this grassland was a tamarack (*Larix laricina*) swamp with acidic, organic soils (Hamerstrom and Hamerstrom 1973). The Wisconsin Dept. of Natural Resources now manages the grassland for threatened Greater Prairie Chickens (*Tympanuchus cupido*) by burning, tillage, and grazing (J. Kier, pers. comm.).

Vegetation data were collected in August 1990 when plants were mature enough to be identified. Following Zimmerman (1988), I chose six square 10-ha plots and sampled vegetation randomly within these plots. Each of the plots contained two linear transects, 324 m in length, separated by at least 18 m. I began these transects randomly 18 m internal to a plot's southern or western border and proceeded along a line perpendicular to that border. Each transect contained a random number ($N = 2-18$) of sample points. (No more than 18 sample points could fit on a transect plot's width.) In all, I established 12 transects and 103 sample points. At each sample point, I recorded percent cover for herbaceous plants, using a 0.10 m Daubenmire frame (Daubenmire 1968). For woody plants, I used a square quadrat (Cottam and Curtis 1956) measuring two m on a side. In the quadrat, I also measured vegetation height using the tallest plant, alive or dead. Vertical density was measured by counting plant contacts on a vertical 12 mm diameter rod. This measurement was made only when wind speed was less than 25 km/h, in order to minimize extraneous plant contacts. Relative importance (I) for each plant type was calculated with Daubenmire values as $I = F + (C/100)$, where F is the plant's frequency of occurrence, expressed as a decimal, and C is its percent coverage. Each vegetative feature was designated as either high value or low value nest cover, following Knapton (1978, 1979, 1980) who found that the sparrows prefer nesting below one m in dense shrubs. The nests I found during vegetation sampling confirmed this preference (Munson, unpubl. data).

I observed an estimated 60–70 unbanded male Clay-colored Sparrows for 16 h in May 1991 to determine territorial boundaries. For each sample point, I made at least two, five-min visits, during which I watched for indications that the point was within a territory. If a bird sang or chased a conspecific intruder, its location was marked on a large-scale map that included, as marks of reference, the 103 sample points. This spot-mapping benefitted from the conspicuous and energetic behavior of territorial males, and consequently there were numerous points of observation per bird. I assumed this technique did not alter the

TABLE 1
RELATIVE IMPORTANCES (I) OF THE FIVE MOST ABUNDANT PLANTS OCCURRING WITHIN
CLAY-COLORED SPARROW TERRITORIES

Plant	Frequency of occurrence (F)	Percent cover (C)	Relative importance (I) ^a
<i>Solidago</i> spp.	0.71	35	1.06
<i>Spiraea alba</i>	0.59	20	0.79
<i>Poa compressa</i>	0.47	29	0.76
<i>Linaria vulgaris</i>	0.57	12	0.69
<i>Phalaris arundinacea</i>	0.27	20	0.47

^a Relative importance was calculated as $F + (C/100)$, where F is frequency of occurrence, expressed as a decimal fraction, and C is percent coverage.

sparrows' behavior, because the birds tolerate human activity (Knapton 1979; Munson, pers. obs.). The minimum convex polygon method (Mohr 1947) was used to infer territorial boundaries from points of observation. I compared habitat inside territories to that outside territories by conducting two-sample *t*-tests for the following measurements: woody stem density, vegetation height, percent coverage by each plant, vertical density, and species richness. To compare frequencies of occurrence for each plant, I used goodness-of-fit chi-square tests.

Results and discussion.—Of 103 sample points, 49 were within and 54 were outside of territories. Fifty-eight kinds of plants were recorded in sampling, 42 of which occurred within territories. The five plants of greatest importance within territories (Table 1) covered 116% of an average territory, a coverage in excess of 100% because leaves overlapped. Some plants of lesser importance, such as *Salix interior*, may still be crucial elements of territories judging from the sparrows' preference for them. Eleven habitat features were "preferred," which I define as more abundant inside than outside of territories. I divided these habitat features into high value and low value nest cover (Table 2). Eight of the 11 preferred habitat features had high value as nest cover. Conversely, none of the three habitat features that were more abundant outside of territories had high value as nest cover. Habitat features not displayed in Table 2 showed no statistical difference between the samples within and outside territories. These habitat features were: percent cover for 44 additional species of plants, stem density for seven species of woody plants, and frequency of occurrence for 53 species of plants.

Clay-colored Sparrows selected territories containing dense stands of woody vegetation and avoided open grasslands. Grasses formed an important vegetative component within territories, but three of the seven recorded grass species were more common outside territories. *Poa compressa* and *Agropyron repens* had greater coverages, and *Phleum pratense* occurred with greater frequency outside of territories (Table 2). I could not relate the importance of woody plants with that of grasses because abundance of grasses was measured in percent cover, whereas woody plants were measured with stem densities. Nevertheless, stem densities for *Salix interior* and *Spiraea alba* were much greater within territories, and their shade may have suppressed the importance of grasses within territories. Thus, the birds' apparent aversion to grasses may have been only an artifact of their selection for woody vegetation.

The results presented in Table 2 support the prediction that in Clay-colored Sparrows preferred habitat features are of high value as nest cover rather than a reflection of what is

TABLE 2
HABITAT WITHIN AND OUTSIDE OF CLAY-COLORED SPARROW TERRITORIES

Habitat feature	Within territories	Outside territories	P ^b
Stem density (m ⁻²)			
<i>Salix interior</i> ^{c,d}	1.8 ± 3.0 ^a	0.02 ± 0.02	<0.0002
<i>Spiraea alba</i> ^{c,d}	7.6 ± 7.4	4.3 ± 8.4	<0.05
Percent cover (%)			
<i>Agropyron repens</i>	10.7 ± 21.4	30.9 ± 35.9	<0.001
<i>Phalaris arundinacea</i> ^c	20.1 ± 37.3	4.1 ± 17.7	<0.01
<i>Poa compressa</i>	29.3 ± 40.1	48.6 ± 42.2	<0.02
Frequency of occurrence			
<i>Salix interior</i> ^{c,d}	0.41	0.02	<0.0002
<i>Phalaris arundinacea</i> ^c	0.27	0.06	<0.02
<i>Spiraea alba</i> ^{c,d}	0.78	0.33	<0.02
<i>Carex</i> sp. ^c	0.08	0.00	<0.05
<i>Phleum pratense</i>	0.12	0.33	<0.05
Other			
Woody species richness ^{c,d}	1.9 ± 1.2	0.6 ± 0.6	<0.0001
Vegetation height (cm) ^{c,d}	186.3 ± 156.9	88.9 ± 17.3	<0.0002
Plant species richness ^{c,d}	5.7 ± 2.1	4.7 ± 1.7	<0.01
Vertical density (contacts) ^{c,d}	7.4 ± 2.3	6.4 ± 2.2	<0.05

^a Mean ± SD.

^b See Methods section for tests used.

^c Value is greater within territories.

^d Habitat feature of high value as nest cover.

available. Only 19% (22 of 118) of the habitat features available to the sparrows had high value as nest cover, and yet 73% (8 of 11) of the habitat features that were more abundant within territories were of high value as nest cover. The disparity is significant ($\chi^2 = 5.52$, $P < 0.02$) and provides evidence that the sparrows choose breeding habitat for its abundance of nest cover.

For the numerous bird species that both nest and forage within their territories, it is difficult to evaluate the relative influences that nest cover and feeding opportunities have on territorial habitat selection (Martin and Roper 1988). In Clay-colored Sparrows, however, individuals leave their territories to forage in a different habitat type (Knapton 1979). It is not known how far the foraging birds travel from their territories, but I have observed sparrows flying hundreds of meters to habitat patches completely disconnected from territories. Therefore, feeding opportunities apparently do not determine territorial habitat selection in this species. I have shown that in the absence of foraging demands, at least for Clay-colored Sparrows, nest cover may become the primary influence on territorial habitat selection. Still, both nest cover and feeding opportunities can conceivably influence avian habitat selection. In most bird species, the two influences likely operate concurrently, but among bird species the relative influences may vary considerably. Territorial habitat selection in Clay-colored Sparrows, evidently determined by nest cover and not food, would fall at an extreme on this continuum of influences.

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Dominance relationships of dabbling ducks wintering in Yucatan, Mexico.—Evolution of dominance behavior in waterfowl may be related to variation in the ability to obtain needed resources (e.g., food). This idea has been used to support hypotheses explaining differential distribution of the sexes (Nichols and Haramis 1980, Hepp and Hair 1984) and inter- and