

## COLONY CHOICE IN CLIFF SWALLOWS: EFFECTS OF HETEROGENEITY IN FORAGING HABITAT

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**ABSTRACT.**—One potential determinant of colony size in birds is the local availability of food near a nesting site. Insectivorous Cliff Swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska nest in colonies ranging from 2 to over 3,000 nests, but they feed on so many kinds of insects that direct sampling of food resources is impractical. Instead, we investigated the degree to which swallow colony size was correlated with the extent of different habitat types, land use diversity, and plant species diversity in the colony's foraging range, and used those parameters as indices of potential variation among sites in food availability. Amount of flowing and standing water in the foraging range was a significant predictor of mean colony size across years at a site, with larger colonies associated with more water. The same result held for most years when analyzed separately. The extent of flowing water in the foraging range also was a significant predictor of the frequency with which a site was occupied across years. In addition, univariate tests suggested that the amount of cultivated cropland in the foraging range varied inversely with colony size. Land use diversity, as measured by Simpson's index, increased significantly with colony size, and all of the sites with perennially very large colonies (mean colony size >1,000 nests) were associated with foraging ranges of relatively high land use diversity. Repeatability of colony size across years differed significantly from zero across all sites, but repeatabilities were significantly lower (colony sizes less similar between years) for sites situated in low-diversity habitats and for sites used less often. There was no strong effect of plant species diversity within the foraging range on either colony size at a site or likelihood of site use. We conclude that land use diversity *per se* (and possibly the extent of water near a site) might influence insect distribution and constrain formation of the larger colonies to certain sites. These findings emphasize that colony choice in Cliff Swallows is complex, reflecting both the socially mediated costs and benefits of group size that vary among individuals and the effects of habitat heterogeneity that may influence food availability at some sites. *Received 27 March 2001, accepted 7 December 2001.*

**RESUMEN.**—Un determinante potencial del tamaño de las colonias de aves es la disponibilidad local de alimento en el área de nidificación. La golondrina *Petrochelidon pyrrhonota* es una especie insectívora que nidifica en el sur oeste de Nebraska (USA) en colonias que fluctúan entre 2 y más de 3000 nidos. Estas golondrinas se alimentan de una gran variedad de insectos, por lo que un muestreo directo de los recursos alimenticios es impracticable. En cambio, investigamos el grado de correlación entre el tamaño de las colonias de golondrinas y la cantidad de diferentes tipos de hábitat, la diversidad de usos del suelo y la diversidad de plantas en el rango de forrajeo de la colonia. Utilizamos estos parámetros como índices de la variación potencial en la disponibilidad de alimento entre sitios. En un sitio determinado, la cantidad de agua corriente y estancada en el área de forrajeo predijo significativamente el tamaño medio de las colonias a través de los años, con colonias más grandes asociadas con una mayor cantidad de agua. Los resultados se mantuvieron para la mayoría de los años al analizar los datos por separado. La cantidad de agua corriente en el área de forrajeo también predijo la frecuencia con que un sitio fue ocupado a través de los años. Además, pruebas univariadas sugirieron que la cantidad de campos de cultivo en el área de forrajeo varió inversamente con el tamaño de la colonia. La diversidad de usos del suelo, medida mediante el Índice de Simpson, aumentó significativamente con el tamaño de la colonia y todos los sitios con colonias permanentes de gran tamaño (tamaño medio >1,000 nidos) estuvieron asociados con áreas de forrajeo con una diversidad de uso de suelo rela-

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tivamente alta. La estabilidad del tamaño de las colonias a través de los años fue significativamente diferente de cero en todos los sitios, pero la estabilidad fue significativamente más baja (tamaños de colonia menos similares entre años) en sitios situados en hábitats de baja diversidad y en sitios ocupados con menor frecuencia. No hubo un efecto marcado de la diversidad de plantas en el área de forrajeo sobre el tamaño de la colonia ni sobre la probabilidad de ocupación de un sitio. Concluimos que la diversidad de uso del suelo *per se* (y posiblemente la cantidad de agua cercana a un sitio) podría influenciar la distribución de insectos y restringir la formación de grandes colonias a sólo ciertos sitios. Estos hallazgos enfatizan la complejidad de la elección de sitios para establecer colonias en las golondrinas. Esta elección refleja tanto los costos y beneficios sociales del tamaño del grupo que varían entre individuos, como los efectos de la heterogeneidad del hábitat sobre la disponibilidad de alimento en algunos sitios.

MOST COLONIALY breeding birds and mammals exhibit wide variation in colony size, with the smallest and largest colonies within a population often varying by several orders of magnitude. Natural variation in colony size has been used in numerous studies to measure consequences of breeding with different numbers of conspecifics, and we now understand many of the costs and benefits of coloniality (e.g. Hoogland and Sherman 1976; van Vesseem and Draulans 1986; Møller 1987; Hoogland 1995; Brown and Brown 1996, 2001). Our understanding of what causes variation in colony size is still quite limited, however. Relatively few hypotheses to explain why animals breed in groups of different sizes have been proposed or tested (Brown et al. 1990). Most workers have tended to attribute variation in colony or group size either to environmental heterogeneity of resources (Horn 1968, Fretwell and Lucas 1970, Leighton and Leighton 1982, Gibbs et al. 1987, Shields et al. 1988, Gibbs 1991, Brown and Rannala 1995, Danchin and Wagner 1997, Gibbs and Kinkel 1997) or to phenotypic differences that predispose individuals to choose large or small colonies (Jones 1987; Ranta and Lindstrom 1990; Hoglund et al. 1993; Ranta et al. 1993; Brown and Brown 1996, 2000, 2001). Both resource-related and social factors may interact in some species to lead to colony formation.

The two most likely environmental determinants of colony size are the extent of physical space for building of nests at a given site and amount of food available near a suitable colony site. Neither has proven easy to measure, especially for vertebrates. The suitability (and thus the amount) of nesting space at a site can seldom be determined objectively, with most workers inferring suitability of breeding habitat from presence or absence of nesting individuals (Brown and Brown 1996, 2001). Direct

measures of food availability have been equally elusive, in part because many colonial animals feed over such large expanses of habitat (Hunt and Schneider 1987) and on so many different kinds of prey that even identifying what to measure and where is often impossible.

Yet understanding the degree to which food availability in particular causes colony formation is important, because ideal-free matching of population density to local resources is regarded as one of the primary ecological determinants of animal spatial distribution (Fretwell and Lucas 1970, Sutherland 1983, Parker and Sutherland 1986, Tregenza 1995, Danchin and Wagner 1997). If colony size reflects heterogeneity in local food availability, evolution of coloniality may have been driven in part by aggregation at resources in a process analogous to the formation of foraging groups in high-yield patches. That in turn could augment the widely studied social benefits of grouping as causes of coloniality, or in some cases might suggest that the social benefits are secondary consequences of high-density nesting (Wittenberger and Hunt 1985, Shields et al. 1988, Barta and Giraldeau 2001, Brown and Brown 2001).

Ecologists have tried with mixed success to establish connections between local food availability and colony size. The best data to date are probably those of Smith (1985), who directly measured flying insect abundance near colonies of orb-web spiders and found that aggregations occurred in areas of high prey availability. The predominant approach in studies of birds has been to measure food availability indirectly by establishing correlations between the amount of presumed foraging habitat and colony size. In herons, colony size varied directly with the extent of wetlands within a colony's foraging range (Gibbs et al. 1987, Farinha and Leitao 1996, Gibbs and Kinkel 1997). Col-

ony size in Rooks (*Corvus frugilegus*) was positively correlated with the amount of nearby meadow and pasture land (Griffin and Thomas 2000). However, other studies on birds have found no strong relationships between habitat characteristics and colony size (Kelly et al. 1993, Butler 1994, Bustamante 1997). Past work has been limited somewhat by not being able to specify ranges from the colony site at which colony residents routinely forage. Previous studies also have tended to focus on only one or a few types of habitat as presumed foraging areas (e.g. Kushlan 1976, Fasola and Barbieri 1978). Selective inclusion of only some habitats may overlook the potential effect of overall habitat diversity on local food abundance.

As part of a long-term study on the evolution of coloniality in Cliff Swallows (*Petrochelidon pyrrhonota*), in this article we explore for the first time the degree to which colony size is related to ecological features of the surrounding habitat. We had the advantage of knowing with certainty the foraging ranges of the birds occupying the colonies, allowing us to study the known foraging habitat without making untested assumptions about where and at what distances colony residents might be feeding. In addition to measuring habitat type and the diversity of habitat (land use) near colonies, we also investigated the degree to which plant species diversity was associated with colonies of different sizes. Because local plant diversity per se may affect the abundance of flying insects (Andow 1991), on which Cliff Swallows exclusively feed, we evaluated whether plant diversity and habitat diversity more generally might lead to predictable changes in overall insect abundance that are important to Cliff Swallows and that might cause birds to settle at a site. We use our results to gain insight into the evolution of coloniality in Cliff Swallows.

#### METHODS

*Study animal and study site.*—Cliff Swallows are highly colonial passerines that breed throughout most of western North America (Brown and Brown 1995). Their gourd-shaped mud nests are attached to the vertical face of cliff walls, rocky outcroppings, or artificial sites such as the eaves of buildings or bridges. Nests tend to be stacked closely, often sharing walls. Cliff Swallows are migratory, wintering in southern South America, and have a relatively short breeding season in North America. At our study site, they arrive beginning in late April or early May, and

most depart by late July. They generally raise only one brood.

Cliff Swallows feed exclusively on flying insects. They are generalist feeders, with dozens of insect families identified in diet samples (Brown and Brown 1996). Foraging generally occurs in groups and, except in cold weather, at altitudes of 50 m or more. The birds cue on the presence of insect swarms transported aloft by localized convection currents, and as a result their food sources are spatiotemporally variable both within and between days (Brown and Brown 1996). Colonies serve as information centers, with birds observing others and following successful individuals to food sources (Brown 1986, Brown and Brown 1996). Past work has shown that virtually all foraging by colony residents (except in bad weather) occurs within a 1 km radius of a colony site, regardless of colony size or habitat type (Brown et al. 1992, Brown and Brown 1996).

Our study site is centered at the Cedar Point Biological Station (41°13'N, 101°39'W) near Ogallala, in Keith County, along the North and South Platte rivers, and also includes portions of Deuel, Garden, and Lincoln counties, southwestern Nebraska. We have studied Cliff Swallows there since 1982. There are ~160 Cliff Swallow colony sites in our 150 × 50 km study area, with about a third of those not used in a given year. In our study area the birds nest on both natural cliff faces and on bridges, buildings, and highway culverts. Colony size within the population varies widely; in southwestern Nebraska, it ranges from 2 to 3,700 nests per site, with some birds nesting solitarily. Over a 20 year period, mean ( $\pm$ SE) colony size ( $n = 1,363$ ) was 363 ( $\pm 16$ ) nests. A colony site tends to be separated from the next nearest by 1–10 km but in a few cases by  $\geq 20$  km. Groups of nests were defined as colonies if the nest owners at least occasionally interacted in foraging or in the mobbing of predators (Brown and Brown 1996); in practice, all the nests on a single bridge or culvert typically constituted a single colony. The study site is described in detail by Brown and Brown (1996).

*Measures of colony size.*—Colony size is the maximum number of nests at a site to contain  $\geq 1$  egg. We determined colony size by doing regular nest checks using a dental mirror and flashlight inserted through each nest's mud neck, or by estimating number of active nests by the number of birds regularly present. Those estimation methods are presented fully in Brown and Brown (1996). Colony size was recorded for each site each year of the study, giving us colony-size and site-use data for up to 19 years at some sites. Fewer years of data were available for sites discovered by us in the later years of the study. In this article, for most analyses we use data for 91 of the ~160 colony sites that have been used since 1982; these 91 were ones for which aerial photographs (see below) were available to us. Of these, we had a smaller subset of 59 sites for which we had plant-diversity data,

chosen to represent the full range in colony size seen in the population.

For our analyses, we first calculated two overall indices of colony size for each site. One was the grand mean of all colony sizes across all years. That measure included zero in the calculation for any year in which the colony site was unoccupied. The grand mean thus reflected both long-term use and relative size of the colony at each site. We also calculated the mean colony size in only the years a site was occupied. However, the grand mean was highly correlated with the mean from only the years used ( $r = 0.99$ ,  $P < 0.0001$ ,  $n = 91$ ). That result, and the fact that all analyses yielded virtually identical conclusions with either index of colony size, led us to restrict the analyses presented here to those using the grand mean of colony size across all years. References to mean colony size in this paper refer to this grand mean unless specified otherwise. Repeatability analyses also included zero for any year in which a site was unused unless specified otherwise. Colony-site use independent of colony size was reflected in the variable, number of years used, in our analyses.

*Characterizing habitat types and land use diversity.*—The habitat near colony sites was quantified from high-resolution aerial photographs supplied by the Aerial Photography Unit of the U.S. Department of Agriculture. Those photos, taken in summer 1993, were overlaid with a transparent acreage grid centered on each colony site. Because Cliff Swallows generally forage within a 1 km radius from the colony site (see above), we designated a circular region of 2 km diameter centered at the colony site in which to classify habitat. That circular region encompassed the equivalent of 1,256 squares on the acreage grid; each full square represented 0.62 acres (0.25 ha). If a square contained more than one habitat type, it was counted as a single habitat type on the basis of what was overlaid by a dot contained in each square of the grid. The entire circular region was considered to represent potential Cliff Swallow foraging space at each site, because the birds were observed foraging over all major habitat types. Within the circular foraging range, we used the acreage grid to determine the total coverage of the following eight habitat types, defined as “flowing water,” the surface area of rivers and creeks; “standing water,” the surface area of lakes and ponds; “roads and buildings,” the surface area of asphalt roads and all artificial structures; “bare earth,” the surface area of dirt roads, sand pits, sand bars, plowed fields, or other unvegetated ground; “trees,” the surface area of deciduous and evergreen (*Juniperus* spp.) tree cover; “marsh,” the surface area of aquatic wetlands; “grassland,” the surface area of prairie vegetated with noncultivated grass (often grazing land); and “crops,” the surface area of cultivated fields (usually wheat [*Triticum*] or corn [*Zea mays*]). Land use around our colony sites appeared to be stable

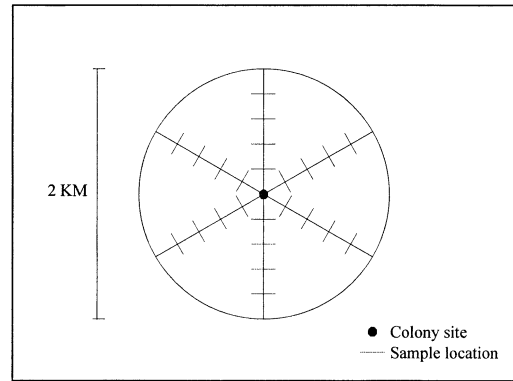


FIG. 1. Schematic representation of vegetation transects at Cliff Swallow colony sites. “Spokes” represent transect lines, and short tick marks are sampling locations.

throughout the years of the study, with no obvious loss or creation of wetlands, cutting of woodlands, or changes in farming or ranching practices. For that reason, we did not try to account for changes in land use at sites between years, and thus we considered the 1993 acreage data as representative for all years. Because the grid overlay was specifically designed to give area in acres, we used acres (rather than hectares) as our unit of measurement in all analyses (1 ha = 2.47 acres).

The extent of land use diversity within the ~778 acre foraging range of each colony was expressed with Simpson’s index of diversity ( $\lambda$ ). The first widely used diversity index in ecology, Simpson’s index is based on proportions and is most appropriate when one has a finite community and all members of the community are censused (Ludwig and Reynolds 1988). That was the case because all acreage in the 2 km diameter circle was categorized and each of the eight habitat types expressed as a proportion. The values of Simpson’s index ( $\lambda$ ) vary inversely with diversity (i.e. lower values indicate higher diversity).

*Characterizing vegetation and plant diversity.*—Vegetation samples were taken in the foraging ranges surrounding 59 colony sites in 1998. Samples were done between 13 May and 24 July. At each site we established six 1 km transects beginning at the center of the colony site’s nesting substrate (e.g. center of bridge or culvert). The first transect headed due north ( $0^\circ$ ), and the rest followed compass headings of 60, 120, 180, 240, and  $300^\circ$  (Fig. 1). Due to dense vegetation cover and water in some areas, and because of time constraints, we did not try to directly measure transect distances. Instead, one observer (C.M.S.) walked a 50 m distance 10 times, counted the number of paces each time, and averaged the counts to give an estimate of pace length. Paces were then counted while walking transects as a measure



of distance, and the same observer conducted all of the vegetation surveys.

Five samples were taken on each transect at 200 m intervals (Fig. 1). An aluminum sampling frame of an "L" shape with dimensions  $2.0 \times 0.5$  m ( $1 \text{ m}^2$ ) gave a rectangular-shaped plot following the recommendation of Bormann (1953). The frame was laid flat on the ground with the short side centered on the transect line and the long side parallel to it. Herbaceous vegetation and low shrubs within the frame were identified to genus. The height of the tallest living plant within each sample, not including any trees over 2 m tall, was measured with a tape measure, and mean plant height for each site was calculated by averaging the tallest plant measured in each sample. If a sample location was covered with water, only vegetation growing above the surface of the water was recorded, and plant height was measured from the water surface. We took a total of 30 samples per colony site (Fig. 1), except in three cases that were missing 2 samples each because the North Platte River prevented completion of the transects. Colonies near a lake included some transects that were all water.

For vegetation diversity, we used the traditional Shannon index of diversity ( $H'$ ). That index was chosen for vegetation analyses because we had only a sample of plants and not a complete count of all individuals in the foraging area. The index was calculated by first adding together the coverage estimates for each genus in all samples taken at a site ( $n$ ) and then dividing this total by the total number of all plants in all samples ( $N$ ). Although the use of  $n_i/N$  produces a biased estimate of the proportion of individuals of the  $i$ th species (or genus), this bias is usually quite small (Peet 1974).

Because the foraging ranges of Cliff Swallow colonies were circular in shape (Brown and Brown 1996), our sets of vegetation samples taken at equal distances from the colony site represent concentric rings of land, each ring increasing in area as the distance from the colony increases (Fig. 1). Both small and large rings were represented by the same number of samples. Because the vegetation types within a foraging range were usually not homogeneous, improper weight might be given to samples (smaller rings) closer to the colony. To determine if that introduced a potential bias, we calculated a Shannon index for each individual sample and compared sample indices in a nonparametric ANOVA according to their distance from the colony. In only 2 of 59 colonies did we find any significant ( $P < 0.05$ ) effect of sample distance on plant diversity. The power of those tests, given only six replicates per distance category per site, was fairly low (14 to 32 with  $\alpha = 0.05$ ,  $k = 5$ ,  $n = 6$ ; Cohen 1988), but because we found no evidence for a consistent difference in diversity measures of samples taken close to versus far from the

colony site, we did not correct or weight diversity measures by distance.

*Statistical analyses.*—We explored relationships between colony size and ecological characteristics of foraging ranges using both multivariate and univariate statistics (see Griffin and Thomas 2000). Linear and logistic multiple regressions were used to rule out certain variables as having little or no effect; those with greater potential explanatory power in the multiple regressions were further examined with univariate tests. We used backward stepwise multiple regressions, beginning with a model containing all variables, and used  $\alpha = 0.10$  for retention in the model. When a regression revealed one or more significant main effects, we checked for interactions with other variables by repeating the regression with the potential interaction terms included in the model. Repeatability was measured with intraclass correlation ( $r_i$ ; Zar 1999). Differences in repeatabilities were inferred by calculating 95% confidence intervals for the intraclass correlation coefficients and looking for overlap of the intervals (Zar 1999). Statistical calculations were done using SAS (SAS Institute 1990).

## RESULTS

*Habitat type and land use diversity of foraging ranges.*—A multiple linear regression of the proportions of the eight habitat types plus Simpson's index of land use diversity within a colony's foraging range revealed that the amount of flowing and standing water within a 1 km radius of the colony site were the only significant predictors of mean colony size at a site over all years of the study (Table 1). When repeating the analysis by year for the 11 year period of 1990–2000, we found generally the same pattern (Table 2): flowing or standing water, or both, were significant predictors of annual colony size at a site in all years individually except 1996 (a year in which large numbers of Cliff Swallows were killed by bad weather early in the season before colony sizes were established; Brown and Brown 1998). These results (Table 1) thus were not artifacts of averaging colony sizes across years. The extent of roads and buildings seemed to be associated with colony size in 5 of the 11 years. The regression coefficients were positive in all cases, suggesting that the amounts of those habitat types tended to increase for larger colonies (Table 2). Similarly, the amount of flowing water in a foraging range was also positively related to the number of years a colony site was occu-

TABLE 1. Results of backward stepwise linear regression of factors potentially predicting mean Cliff Swallow colony size at a site ( $n = 91$  sites). Variables with  $P > 0.10$  are shown at the step at which they were removed from the regression model. We found no significant interaction terms.

Variable	Regression coefficient	SE	F	P
Marsh	0.013	0.943	0.00	0.99
Crops	-0.013	0.943	0.00	0.99
Bare earth	0.866	4.079	0.05	0.83
Simpson's index	-237.199	840.357	0.08	0.78
Trees	-0.252	0.642	0.15	0.70
Grassland	0.443	0.400	1.22	0.27
Roads and buildings	0.980	0.905	1.17	0.28
Flowing water	7.300	2.132	11.72	<0.001
Standing water	1.345	0.447	9.07	0.003

pied (Table 3), suggesting that site use per se was related to the extent of river or creek habitat at a site.

Univariate tests showed the same trends, with positive significant correlations between the amount of flowing and standing water and mean colony size over all years (Fig. 2). The extent of roads and buildings, apparently a predictor of colony size in some years (Table 2), showed no significant correlation with mean colony size in a univariate test (Fig. 3a). Although it was not a significant predictor variable in the multiple regression, we found a significant univariate negative correlation between amount of cultivated cropland in the foraging range and mean colony size (Fig. 3b). The amount of grassland, marsh, bare earth, or trees had no apparent effect on mean colony size in either the multivariate or univariate analyses. For colony-site use, we found in univariate tests that the number of years a site was occupied ( $n = 91$  sites) increased significantly with the amount of flowing water ( $r = 0.28$ ,  $P = 0.008$ ), roads and buildings ( $r = 0.22$ ,  $P = 0.039$ ), and trees ( $r = 0.23$ ,  $P = 0.027$ ) within the foraging range.

The extent of land use diversity within a foraging range, as measured by Simpson's index, was not significantly associated with mean colony size in the multivariate regression (Table 1), but the diversity index declined significantly with colony size in a univariate analysis (Fig. 4). Because a lower index means greater diversity, it appeared that extent of land use diversity varied directly with colony size. The same pattern applied to colony use: the number of years a site was occupied was inversely related to Simpson's index ( $r = -0.21$ ,  $P = 0.047$ ,  $n = 91$  sites). All of the sites with perennially very large colonies (mean >1,000 nests) were asso-

ciated with foraging ranges containing relatively high land use diversity (Fig. 4). Comparing the 7 colony sites with mean colony sizes >1,000 nests with the 84 sites with mean colony sizes <1,000 nests, the large colonies had significantly lower Simpson's indices (higher land use diversity), less grassland, and more roads and buildings within their foraging ranges (Table 4). The trends for the other variables were consistent with our other analyses (Table 1, Fig. 3b), with more flowing and standing water and less cropland associated with the larger colonies (Table 4).

If foraging habitat near a colony site is a determinant of colony size, one might expect similar colony sizes at a site between years. Repeatability of colony size at a site was high and significantly different from zero for all colony sites from 1982-2000 combined ( $n = 172$  sites, including many for which we had no aerial photograph data):  $r_t = 0.946$ ,  $P < 0.0001$ . Thus, when including years of nonuse as colony sizes of zero, Cliff Swallow colony use and size tended to be similar at a site from year to year. When restricting the analysis only to years when each site was occupied, repeatability of colony size was lower but still significantly different from zero:  $r_t = 0.883$ ,  $P < 0.0001$ . This repeatability differed significantly from the repeatability calculated from all years (95% CI of 0.856-0.903 and 0.945-0.947), suggesting that some of the annual consistency at a site derives from the probability of site use independent of colony size per se.

We detected a relationship between repeatability of colony size and the number of years a site was used. In using only years in which a site was active (excluding colony sizes of zero), repeatability increased significantly the more

TABLE 2. Summary of results from backward stepwise linear regressions by year of factors potentially predicting Cliff Swallow colony size at a site. Only variables with  $P < 0.10$  are shown.

Year	<i>n</i> (No. sites)	Variable	Regression coefficient	SE	<i>F</i>	<i>P</i>
1990	74	Flowing water	7.085	4.074	3.02	0.09
		Standing water	1.405	0.725	3.76	0.06
1991	75	Roads and buildings	2.727	1.388	3.86	0.05
		Flowing water	9.874	3.591	7.56	0.008
1992	78	Standing water	1.503	0.632	5.67	0.020
		Flowing water	7.416	3.586	4.28	0.042
1993	83	Standing water	1.569	0.663	5.59	0.021
		Flowing water	9.056	3.235	7.84	0.006
1994	85	Standing water	1.486	0.614	5.86	0.018
		Flowing water	9.911	2.823	12.30	<0.001
1995	88	Standing water	1.127	0.538	4.38	0.039
		Roads and buildings	1.941	0.979	3.93	0.05
1996	92	Flowing water	7.417	2.374	9.76	0.002
		Standing water	0.971	0.448	4.70	0.033
1997	91	Roads and buildings	1.657	0.053	9.90	0.002
		Roads and buildings	1.220	0.703	3.01	0.09
1998	88	Flowing water	4.982	1.703	8.56	0.004
		Standing water	0.775	0.309	6.27	0.014
1999	90	Flowing water	6.268	2.175	8.31	0.005
		Standing water	1.071	0.418	6.56	0.012
2000	86	Flowing water	7.419	2.326	10.17	0.002
		Standing water	0.960	0.452	4.51	0.036
2000	86	Roads and buildings	1.962	0.551	12.66	<0.001
		Standing water	2.759	1.048	6.93	0.010

often a site was used (Fig. 5). Thus, colony sites that were more rarely used tended to vary more in size from year to year; perennially used sites had more consistent colony sizes between years.

We also divided colonies into ones with relatively high and low land-use diversity within

TABLE 3. Results of backward stepwise linear regression of factors potentially predicting the number of years a Cliff Swallow colony site was occupied ( $n = 91$  sites). Variables with  $P > 0.10$  are shown at the step at which they were removed from the regression model. We found no significant interaction terms.

Variable	Regression coefficient	SE	<i>F</i>	<i>P</i>
Simpson's index	-1.548	11.608	0.02	0.89
Bare earth	-0.015	0.056	0.07	0.79
Crops	0.015	0.056	0.07	0.79
Marsh	0.007	0.012	0.40	0.53
Grassland	0.003	0.005	0.29	0.59
Standing water	0.006	0.006	0.88	0.35
Trees	0.012	0.008	2.03	0.16
Roads and buildings	0.019	0.012	2.55	0.11
Flowing water	0.077	0.028	7.50	0.007

their foraging ranges. High-diversity sites ( $n = 71$ ) were arbitrarily defined as those with Simpson's indices  $< 0.500$  and low-diversity sites ( $n = 20$ ) as those with indices  $\geq 0.500$  (see Fig. 4). Repeatability of colony size ( $\pm 95\%$  CI) over all years for the high-diversity sites was 0.955 ( $\pm 0.939$ -0.967), compared to 0.743 ( $\pm 0.558$ -0.856) for the low-diversity sites. Thus, colony sites surrounded by greater habitat diversity tended to be more consistent in their use and colony size from year to year.

*Plant diversity of foraging ranges.*—Because plant diversity was measured in 1998 only and is subject to annual variation caused by climatic conditions, differential rates of grazing, or other factors, we restricted our comparison of plant diversity and colony size and use to the 1998 season only. We included the effect of sampling date in case annual growth over the summer might have affected diversity measures. In a multivariate analysis, colony size was unrelated to tree size, herbaceous plant height, or plant diversity within the foraging range, and there was no relationship between the date that we sampled those colonies and colony size (Table 5). We also found no significant univariate (Pearson) correlations between

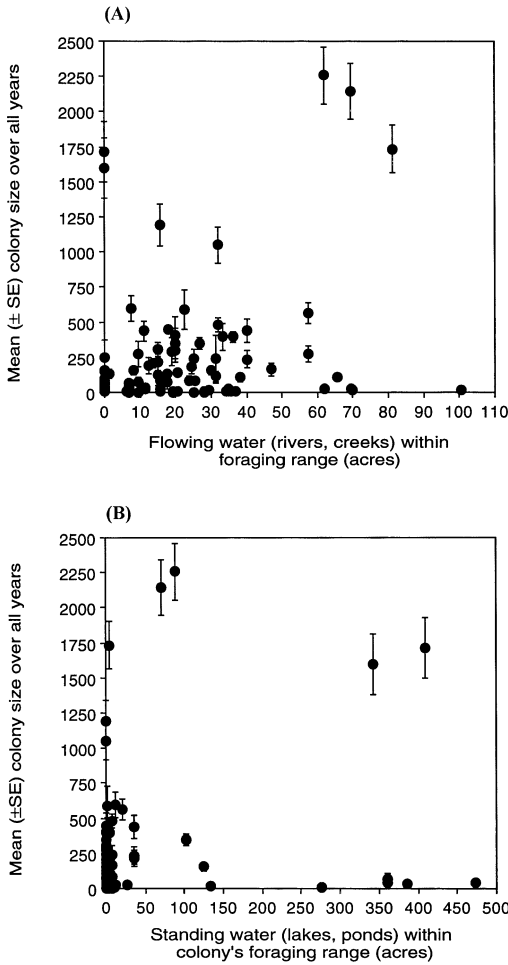


FIG. 2. Mean ( $\pm$ SE) Cliff Swallow colony size at a site in relation to the amount of (A) flowing water (rivers, creeks) and (B) standing water (lakes, ponds) within the colony's 778 acre foraging range. Colony size increased significantly with the amount of flowing water ( $n = 91$  sites,  $r = 0.27$ ,  $P = 0.008$ ) and standing water ( $n = 91$ ,  $r = 0.22$ ,  $P = 0.033$ ) in the foraging range.

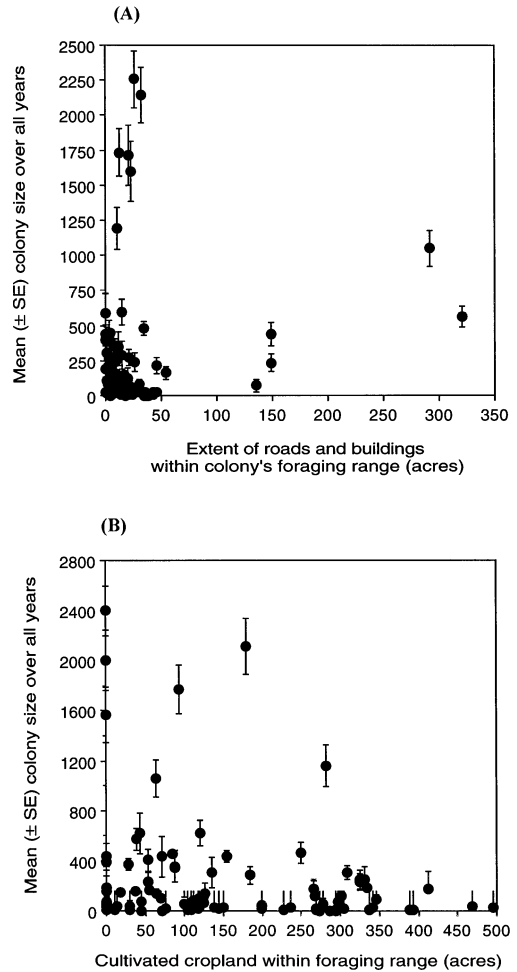


FIG. 3. Mean ( $\pm$ SE) Cliff Swallow colony size at a site in relation to the amount of (A) urban habitat (roads and buildings) and (B) cultivated cropland within the colony's 778 acre foraging range. Colony size did not vary significantly with amount of urban habitat in the foraging range ( $n = 91$  sites,  $r = 0.16$ ,  $P = 0.12$ ) but decreased significantly with the amount of cultivated cropland ( $n = 91$ ,  $r = -0.21$ ,  $P = 0.048$ ).

these variables and 1998 colony size ( $P \geq 0.11$  on all). Plant height increased significantly with date ( $n = 59$ ,  $r_s = 0.59$ ,  $P < 0.0001$ ), as might be expected; measures of plant diversity declined significantly with date ( $n = 59$ ,  $r_s = -0.26$ ,  $P = 0.048$ ), but we found no significant interactions between date, diversity, or plant height and colony size.

Plant diversity was a weak predictor ( $P = 0.08$ ) of colony-site use per se in 1998, but neither tree size nor herbaceous plant height was

related to whether Cliff Swallows occupied a site (Table 6). Date of sampling was also related weakly to site use (Table 6), with unused sites being sampled on average about 7 days later in the summer. However, we found no significant interaction between date and diversity. Mean ( $\pm$ SE) plant diversity as measured by the Shannon index was lower in foraging ranges of used sites ( $2.774 \pm 0.048$ ) than unused sites ( $2.888 \pm$



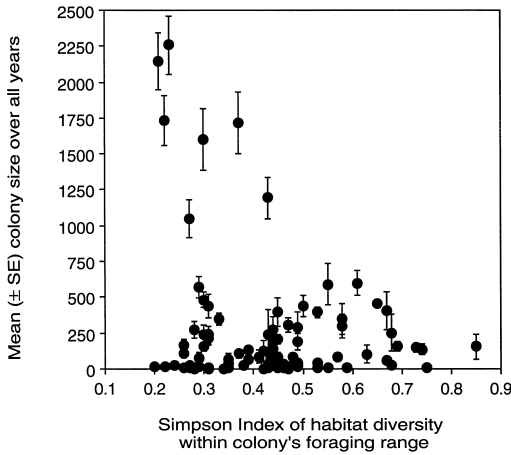


FIG. 4. Mean ( $\pm$ SE) Cliff Swallow colony size at a site in relation to the land-use diversity of its foraging range as measured by Simpson's index. Lower values of the index indicate higher diversity. Colony size declined significantly in areas of lower diversity ( $n = 91$  sites,  $r = -0.22$ ,  $P = 0.040$ ).

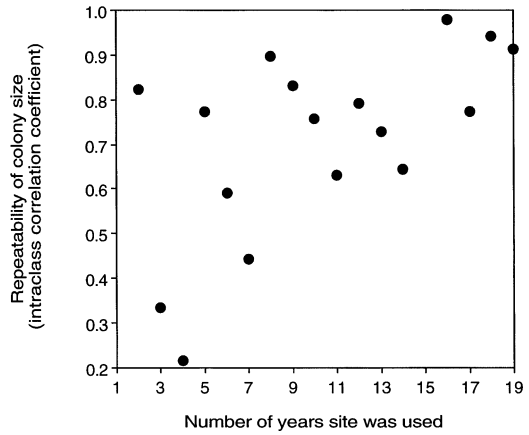


FIG. 5. Repeatability of Cliff Swallow colony size in the years a site was used as measured by the intraclass correlation coefficient ( $r_i$ ) in relation to the number of years a site was used. Repeatability significantly increased with the number of years used ( $n = 17$ ,  $r = 0.59$ ,  $P = 0.013$ ). Each repeatability except for that at 4 years differed significantly from zero ( $F$  tests,  $P \leq 0.03$  on all;  $P = 0.18$  for year 4).

0.074), but in a univariate test that difference was not significant (Wilcoxon test,  $P = 0.15$ ).

DISCUSSION

This study is among the few on terrestrial colonial birds to quantify all habitat types in the known foraging ranges of colonies of different sizes and to have tested whether environmental heterogeneity in foraging habitat has any potential effect on colony choice. On balance, we found consistent though somewhat weak relationships between habitat characteristics and colony size. The patterns were clear

enough, however, to provide some new insight into the evolution of coloniality in Cliff Swallows.

*Habitat type and land-use diversity in relation to colony size.*—Habitat comparisons of foraging areas of colonies revealed that the amount of flowing and standing water was a significant predictor of colony size in most years, with more water near larger colonies. The presence of water also seemed related to the likelihood that a colony site would be used in a given year. Although none of the other habitat types were consistently associated with larger colonies,

TABLE 4. Comparison of 7 colony sites supporting mean colony sizes >1,000 nests with 84 colony sites supporting mean colony sizes <1,000 nests. Except for Simpson's index, means reflect the amount (acres) of each habitat type within a colony's foraging range.

Variable	>1,000 nests		<1,000 nests		$P^a$
	Mean	SE	Mean	SE	
Marsh	51.3	28.6	22.7	6.8	0.13
Crops	88.4	40.8	151.9	14.2	0.18
Bare earth	26.2	5.4	19.6	1.4	0.22
Simpson's index	0.290	0.031	0.442	0.014	0.002
Trees	117.7	17.5	85.4	8.1	0.10
Grassland	273.9	27.6	414.0	15.2	0.006
Roads and buildings	59.5	38.7	22.6	4.5	0.05
Flowing water	37.2	12.8	19.9	2.1	0.25
Standing water	130.8	65.0	48.7	13.2	0.10

<sup>a</sup> Based on Wilcoxon test for each row.

TABLE 5. Results of backward stepwise linear regression of factors related to plant diversity as potential predictors of Cliff Swallow colony size at a site in 1998 ( $n = 59$  sites). Variables are shown at the step at which they were removed from the regression model. We found no significant interaction terms.

Variable	Regression coefficient	SE	F	P
Tree size	-5.165	6.745	0.59	0.45
Date sampled	-5.004	4.752	1.11	0.30
Plant height	1.957	3.301	0.35	0.56
Plant diversity (Shannon index)	-318.337	221.266	2.07	0.16

the biggest colonies were all situated in areas that provided relatively high diversity in land use within their foraging ranges. Surprisingly, larger colonies if anything were less likely than small colonies to contain large amounts of cropland within their foraging ranges, and we had expected monocultures (and their associated greater insect abundances; see below) to be more closely associated with larger colonies.

Do these results reflect differences among sites in food availability and thus represent possible determinants of colony size? Some of our results did not suggest any important food-related habitat differences among sites. For example, because Cliff Swallows typically feed high above the ground on insects concentrated in thermals, we might expect availability of insects they feed on to be greatest in areas of bare earth or grasslands, topography that is especially favorable for the formation of thermals and localized convection (Wallington 1961, Drake and Farrow 1988). Neither of those habitat types had any association with colony size and thus no apparent effect on food availability. Further, because there was no relationship between extent of marsh and colony size, it would not appear that marshland (generally regarded as one of the more productive terrestrial habitats in terms of insects; Orians 1980, Jackson and Fisher 1986, Gray 1989a) led to any localized increase in food availability or at least to any increase that Cliff Swallows were sensitive to in forming colonies.

However, our results on the extent of water in foraging areas of colonies provided some weak support for the possibility that food might have influenced colony size at some sites. Streams and standing water are often thought

TABLE 6. Results of backward stepwise logistic regression of factors related to plant diversity as potential predictors of whether a Cliff Swallow colony site was occupied in 1998 ( $n = 59$  sites). Variables with  $P > 0.10$  are shown at the step at which they were removed from the regression model. We found no significant interaction terms.

Variable	$\chi^2$ (df = 1)	P
Plant height	0.14	0.71
Tree size	0.89	0.35
Plant diversity (Shannon index)	2.97	0.08
Date sampled	3.06	0.08

to be associated with insect availability, providing breeding sites for a variety of taxa (Orians 1980, Gray 1989a), and some of the insect families Cliff Swallows are known to feed on (Brown and Brown 1996) have aquatic larval stages. Although Cliff Swallows feed directly over water relatively rarely, primarily taking aquatic or littoral insects only in bad weather when foraging conditions are poor (Brown and Brown 1996), studies have shown that insects tend to be exported from riparian stream habitats to adjacent areas where they may serve as food for birds (Jackson and Fisher 1986; Gray 1989b, 1993). Whether Cliff Swallows routinely feed on insects exported from nearby water is unknown. On the other hand, large expanses of water may inhibit the development of thermals that are created when air rises above warm earth, and consequently expanses of water may also reduce Cliff Swallow foraging opportunities.

Colony size was perhaps more likely affected by the habitat diversity surrounding a site. Aerial insects such as the small dipterans and hymenopterans on which Cliff Swallows feed tend to drift when wind speeds exceed their maximum flight velocity (Lewis 1967, Johnson 1969, Drake and Farrow 1988), and as a result aerial insects can decline in uniformly open areas such as cropland or grassland, especially in windy weather. Aerial insects often concentrate around windbreaks such as hillsides, tree lines, or buildings, and sometimes increase in abundance in fields that are protected by windbreaks such as rows of tall trees (Lewis 1965, 1967, 1969, 1970; Pasek 1988). Insect abundance tends to be greater along the edges of forests or strips of riparian vegetation than in more exposed areas (Helle and Muona 1985, Whitaker et al. 2000). Because moderate to strong wind

is pervasive in our Nebraska study area, it seems probable that habitat diversity that creates edges and thus potential windbreaks for insects can lead to greater food availability for Cliff Swallows. The type of habitat per se may be less important than overall structural diversity, and that is consistent with our finding that the larger colonies formed in areas of greater land-use diversity. Furthermore, because habitats that include buildings create the most edge (at least with respect to windbreaks), their positive association with larger colonies in some years makes sense if colony size is related to windbreak-driven food availability. Similarly, more cropland in a foraging range will result in less edge, explaining perhaps in part the negative relationship between extent of cropland in a foraging range and colony size.

Colony sizes were more consistent from year to year at sites that were perennially occupied. That would be the case if some areas supported more stable food sources from year to year on which the birds could reliably cue. Less stable areas that were less predictably occupied tended to support colonies that varied more widely in size. Again, land-use diversity may have contributed to that pattern, because we found less annual consistency in colony size at sites with low habitat diversity. As habitat diversity (i.e. extent of edge) increases, that may promote more stable food sources for Cliff Swallows in a local area and more consistent colony sizes.

*Plant diversity as an index of food availability.*— It has been known for at least 30 years that plant diversity can affect the distribution and abundance of insect herbivores. For example, studies by Tahvanainen and Root (1972), Bach (1980a,b), and Risch (1980) showed that beetle numbers and density were greater in crop monocultures than in polycultures, and similar results were found for leafhoppers (Power 1987) and alfalfa weevils (Norris et al. 1984). A review by Andow (1991) of 209 published studies, mostly of agroecosystems, identified 287 herbivorous insect species, of which 51.9% were shown to be more abundant in monocultures than in polycultures. Only 15.3% were more abundant in diverse communities (12.5% showed no difference). That result is usually attributed to diverse plant communities supporting more kinds of insect predators and parasites, or pest insects tending to concentrate in

monocultures where the attractive stimuli of many suitable food sources alters insect movement and makes them less likely to leave (Root 1973, Andow 1991).

The expectation that less diverse plant communities would lead to higher insect numbers was the basis for our studying plant diversity of Cliff Swallow foraging ranges. Most of the cultivated land near our colonies consisted of large monocultures, primarily wheat and corn. We thus expected to find relationships between plant diversity and colony size if food availability was important to the birds in colony formation. However, we found no effect of plant diversity within foraging ranges on colony size and only a weak effect on site use; indeed, we found that the extent of cropland (monocultures) declined with colony size. This seems to rule out any effect of monocultures and their associated insect abundance in causing formation of large swallow colonies. It is of course possible that plant diversity within our study area had no effect on insect abundance, but the evidence from other studies of agroecosystems makes that seem unlikely. It is more likely that any effect of plant diversity on insect abundance was simply not important to Cliff Swallows in choosing colonies. In addition, some of any increase in insect abundance in monocultures may have occurred among larval stages that are restricted to the leaves and stems of the plants themselves and which Cliff Swallows would not have encountered while foraging.

*Food availability and the evolution of coloniality.*— The only studies in birds to show strong positive relationships between extent of apparent foraging habitat near colonies and colony size were those of Great Blue Herons (*Ardea herodias*) in Maine and Illinois (Gibbs et al. 1987, Gibbs and Kinkel 1997), and Cattle (*Bubulcus ibis*) and Little (*Egretta garzetta*) egrets in Portugal (Farinha and Leitao 1996). On the other hand, habitat correlations in colonial Rooks (Griffin and Thomas 2000) are hard to interpret due to uncertainty as to the birds' actual foraging ranges and the extent of their use of the habitats in question for foraging. Other studies in birds have found no clear relationships between apparent foraging habitat and colony size (Kelly et al. 1993, Butler 1994, Bustamante 1997). That so few people have explored the role of habitat heterogeneity in the evolution of avian coloniality is perhaps surprising given

the presumed importance of food distribution in structuring other sorts of animal groups (e.g. Leighton and Leighton 1982, Terborgh 1983, Milinski 1988, Tregenza 1995).

Our results (e.g. Figs. 2, 3) suggest that the extent of different foraging habitats may at least influence the variation in colony size among sites. The strongest conclusion appears that the larger colonies are associated with relatively diverse habitats as foraging ranges, and sites in areas of higher land-use diversity are more likely to be occupied in a given year. However, some small and erratically occupied colonies also occur in highly diverse areas, suggesting that land-use diversity and the pattern of food availability that results do not always lead to large colonies or regular site use. One possibility of course is that colony size is indeed closely matched to local food availability but that our measures of habitat and diversity in foraging ranges were unrelated to insect abundance. That seems unlikely, however, given the known responses of insects to both plant species diversity and land-use type and diversity (see above).

Colony-size variation in Cliff Swallows and other birds may also be caused by other ecological factors, including nesting-site availability or the distribution of predators. Large colonies require enough nesting substrate to support many nests, and possibly the small colonies in productive (diverse) foraging areas could be limited in size by the substrate. That seems unlikely for Cliff Swallows, however, because in earlier analyses we found no relationship between colony size and amount of nesting substrate at a site (Brown and Brown 1996). By measuring nesting substrate on bridges and culverts, whose concrete walls tend to be uniform, we could objectively measure nesting-site suitability and availability. Some small colonies occurred on relatively large substrates and some large colonies on relatively small substrates (Brown and Brown 1996). Similarly, we have found no evidence for heterogeneity in the distribution of predators among sites. Nest predation (mostly by snakes) is relatively rare in Cliff Swallows and does not seem to be of sufficient importance by itself to have driven the evolution of coloniality in these birds (Brown and Brown 1996).

Cliff Swallow colony size is known to reflect distributions of individuals whose phenotypic

characteristics vary with group size. For example, these birds' colony-size preferences show moderate heritable variation, reflecting probable correlations between preference and ability to function physiologically or behaviorally in different social environments (Brown and Brown 2000). The analyses in this paper suggest that foraging-habitat heterogeneity may also play some, albeit perhaps small, role in colony choice. Because colony sizes were larger and more consistent (repeatable) between years in areas with high land-use diversity, it may be that food availability constrains formation of large Cliff Swallow colonies to certain areas. These results add to others that suggest that colony choice in Cliff Swallows is complex, with the process including genetic predispositions to certain group sizes, assessment of one's own and others' past reproductive success at a site, attraction by naïve birds to conspecifics, and direct assessment of how environmental factors such as ectoparasites affect site suitability (Brown and Brown 1986, 1996, 2000; Brown and Rannala 1995; Brown et al. 2000).

We urge that the approach we used here be adopted with other colonial birds. Many of the indirect, more behavioral measures of ecological food availability employed in past studies (e.g. food delivery rates, clutch size, mass of adults or chicks) are confounded with bird quality and thus inconclusive (Brown and Brown 2001). However, ecological measures of foraging habitat are independent of individual performance and may come closer to describing the degree of environmental heterogeneity (if any) in food distributions among sites. We also urge that more conceptual and theoretical attention be given to whether we would even expect colony size to reflect local food availability. In light of Gibbs' (1991) heron data showing that the amount of foraging habitat per capita declined in larger colonies even when the total availability of habitat increased, we may need to ask whether food abundance can ever increase proportionately enough with colony size such that large colonies are not actually costly in terms of reduced per capita food intake.

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