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Effects of artificial perches and interspecific interactions on patch use by wintering raptors

Daniel H. Kim, Felipe Chavez-Ramirez, and R. Douglas Slack

Abstract: We used an experimental approach to investigate the effects of woody vegetation and interspecific interactions on patch use by three wintering raptor species in the coastal prairie in south Texas. We manipulated perch type and density by the addition of artificial perches to patches of coastal prairie grasslands, varying perch height in the first year and canopy density in the second year. American Kestrels (*Falco sparverius*) used areas with artificial perches more often than they used natural woody vegetation and areas without woody perches. Northern Harrier (*Circus cyaneus*) patch use did not vary with treatment type. Loggerhead Shrikes (*Lanius ludovicianus*) used areas of natural woody vegetation more than patches with artificial perches and patches with no perches. Patch use by Loggerhead Shrikes was also influenced by the presence of complex woody vegetation and interspecific interactions, whereas American Kestrel use was limited by landscape matrix and ground cover density. We believe that predation by Northern Harriers limited Loggerhead Shrikes to patches with escape cover, while competition from American Kestrels prevented Loggerhead Shrikes from concurrent patch use.

Résumé : Une approche expérimentale nous a permis d'étudier les effets de la végétation ligneuse et des interactions interspécifiques sur l'utilisation des parcelles chez trois espèces de rapaces qui hivernent dans la prairie côtière du sud du Texas. Nous avons manipulé les types et la densité des perchoirs en ajoutant des perchoirs artificiels dans des parcelles de prairie herbeuse côtière; la première année, nous avons fait varier la hauteur des perchoirs et, la seconde année, modifié la densité de la couverture végétale. Les crécerelles d'Amérique (*Falco sparverius*) utilisent plus fréquemment les parcelles avec des perchoirs artificiels que la végétation ligneuse naturelle et les parcelles sans perchoirs ligneux. L'utilisation des parcelles par les busards Saint-Martin (*Circus cyaneus*) ne varie pas d'un traitement expérimental à l'autre. Les pies-grièches migratrices (*Lanius ludovicianus*) utilisent les zones de végétation ligneuse naturelle plus que les parcelles avec des perchoirs artificiels ou celles sans perchoir. L'utilisation des parcelles par les pies-grièches migratrices est aussi influencée par la présence d'une végétation ligneuse complexe et par les interactions interspécifiques, alors que l'utilisation faite par les crécerelles d'Amérique est limitée par la matrice du paysage et la densité de la couverture végétale au sol. Nous croyons que la prédation exercée par les busards Saint-Martin a restreint les pies-grièches migratrices aux parcelles qui possèdent une couverture pouvant servir de refuge et que la compétition par les crécerelles d'Amérique a empêché les pies-grièches migratrices d'utiliser concurremment les mêmes parcelles.

[Traduit par la Rédaction]

Introduction

The primary factor restricting many nonbreeding raptor populations may be food limitation (Newton 1979), which places a premium on efficient foraging. Because sit-and-wait predation by perched birds is extremely energy efficient, Enderson (1960) speculated that limited access to quality hunting perches and roosting sites limited the abundance of

wintering American Kestrels (*Falco sparverius*) in Indiana. However, interspecific interactions may also play an important role in determining the distribution of other wintering raptor species (MacArthur 1958; Paine 1966; Menge and Sutherland 1987; Hakkarainen and Korpimäki 1996). Despite this possibility, few studies have examined the impacts of both competition and predation, either by design or through serendipity. Furthermore, the ecology of nonbreeding avian

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communities remains poorly understood because of a lack of carefully designed experiments. To address these issues, we used an experimental approach to test whether factors limiting local populations of three sympatric raptor species are contingent upon resource availability and ecological interactions within and between species.

Understanding the ecology of wintering populations is fundamentally important for understanding avian population dynamics. For instance, winter habitat quality affects body condition of nonbreeding birds and, more importantly, future reproductive success (Yosef and Grubb 1994; Sherry and Holmes 1996; Sillett et al. 2000). Removal studies have also yielded evidence of intense competition for preferred habitat, implying that access to high-quality wintering sites may be density dependent (Marra et al. 1993). Sexually mediated habitat segregation, a common pattern for both raptors and passerines, implies competition for quality habitat, especially when the larger sex occupies the preferred habitat (Newton 1979; Smallwood 1987; Sherry and Holmes 1996; Ardia and Bildstein 1997).

The south Texas raptor assemblage is species rich, but American Kestrels (110 g), Northern Harriers (*Circus cyaneus*) (325 g), and Loggerhead Shrikes (*Lanius ludovicianus*) (40 g) numerically dominate grassland habitats. All three species display territoriality during the winter season (Cade 1955; Smallwood 1987, 1988; Temeles 1994; Yosef and Grubb 1994; Yosef 1996). Furthermore, wintering Loggerhead Shrikes and American Kestrels use sit-and-wait hunting tactics and show species-specific habitat preferences and nonrandom spacing along roadsides (Bildstein and Grubb 1979; Gawlik and Bildstein 1995).

These patterns suggest possible shortages of high-quality hunting stations. Several studies have investigated habitat quality of raptors by providing additional perching substrate. In Oregon, time spent foraging increased in perch-enriched patches for American Kestrels but not for Northern Harriers (Wolff et al. 1999). Yosef and Grubb (1994) found that perch addition resulted in smaller Loggerhead Shrike territories of superior quality, but Chavez-Ramirez et al. (1994) reported that Loggerhead Shrikes did not prefer artificial perching structures to native herbaceous vegetation, nor did they prefer mown grass to native grasslands as found in other studies (Gawlik and Bildstein 1993; Yosef and Grubb 1994; but see Prescott and Collister 1993).

The influence of interspecific interactions upon habitat use has been recognized in many studies (Newton 1979; Dhont and Eyckerman 1980; Grubb and Greenwald 1982; Garcia 1983; Wiens 1989; Hakkarainen and Korpimäki 1996; Krams 1996). Detecting such interspecific competition is difficult because of the rarity of direct competitive interactions observed in nature (Connell 1983; Schoener 1983; Wiens 1989), but a shift in resource use by a species in the presence of a potential competitor is a strong indication of competitive interactions (Wiens 1989). While competition and predation may regulate resource use by species within and among years, predation appears to have a greater impact on species assemblages than competition (see Sih et al. (1985) for a review; Menge and Sutherland 1987; Hakkarainen and Korpimäki 1996). Risk of predation affects habitat use of many avian and mammalian species by restricting individuals to areas with, or near, escape cover (Caraco et al.

1980; Grubb and Greenwald 1982; Brown 1988; Lin and Batzli 2001). Owing to their small size, shrikes may be restricted to areas that provide refuge from avian predation.

Our objective was to determine what processes limit winter raptor densities at native coastal prairie sites in south Texas. We examined the effects of woody structure on patch use and interspecific interactions of American Kestrels, Northern Harriers, and Loggerhead Shrikes. We address three specific questions regarding wintering raptors at coastal prairie sites. (1) Is the abundance of American Kestrels and Loggerhead Shrikes limited by the availability of perches? (2) Is perch quality associated with perch height and complexity of the perch canopy? (3) Do larger species displace smaller species through predatory and (or) competitive interactions?

We predicted that both male and female American Kestrels would interfere with patch use by Loggerhead Shrikes, while Northern Harriers should impose both competitive and predatory pressures upon Loggerhead Shrikes and American Kestrels. Since the timing of migration differs among these three species, individuals arriving early may defend plots from conspecifics monopolizing patches throughout the winter (Fretwell and Lucas 1970). If early arriving individuals (Loggerhead Shrikes) cannot exclude later arriving individuals (American Kestrels), the larger American Kestrel should usurp the patch from the smaller Loggerhead Shrike, forcing Loggerhead Shrikes to shift to areas that provide escape cover or areas without woody structure for perching. Likewise, female American Kestrels often migrate earlier than males, and Smallwood (1987) found that early arriving females captured and maintained high-quality wintering territories. If the same pattern holds true for south Texas, female American Kestrels should use our artificial perches to a greater extent than males.

Methods

Study sites

We examined native coastal prairie sites at Matagorda Island National Wildlife Refuge and State Park in Calhoun County, Texas (28°6'N, 96°40'W) and the Norias Division of the King Ranch in Kenedy County, Texas (26°40'N, 97°40'W). Matagorda Island is a barrier island of approximately 55 000 ha on the gulf coast of Texas. Vegetative associations include salt marshes, sand dunes, and upland barrier flats. Coastal prairies were confined to the upland flats (Chavez-Ramirez et al. 1994) and were dominated by marshhay cordgrass (*Spartina patens*), gulfdune paspalum (*Paspalum monostachyum*), and seacoast bluestem (*Schizachyrium scoparium*). Woody vegetation was scattered throughout the study site, and was mainly composed of mesquite (*Prosopis glandulosa*) and eastern baccharis (*Baccharis halimifolia*). Norias covers 100 000 ha and was managed for cattle, agriculture, and wildlife. Woody vegetation was prominent and encroached upon grassland areas. Dominant vegetation included marshhay cordgrass and seacoast bluestem with mesquite, huisache (*Acacia farnesiana*), and small stands (0.25–4 ha) of live oak (*Quercus virginiana*) (known as mottes) comprising the majority of the woody structure. The coastal prairie at Norias was bounded by live oak forest and the Laguna Madre.

Plot types

All plots were 100 m × 100 m (1 ha) in area. Experimental treatment consisted of the addition of 25 artificial perches spaced at 25-m intervals in a 5 × 5 grid. Each artificial perch consisted of a mesquite branch affixed to either a wooden fence post or a metal t-post to standardize perching substrates. There were three types of manipulations in 1999: tall perches (over 2.5 m), short perches (under 1.5 m), or a 50:50 mix of both. There were two types of controls: open controls (grassland with no woody vegetation above 1 m) and woody controls (areas with several natural woody perches at heights greater than 1 m) totaling 20 plots at each study site. In 2000, we eliminated the open controls and the height differences, focusing instead on the presence of natural woody brush (woody controls), artificial dense brush (brushy manipulations), and simple perches (regular manipulations) for a total of 12 plots at each study site. Simple perches were constructed as previously noted, while artificial dense (brushy) perches were constructed of three or more mesquite branches to create a more complex canopy. Each brushy plot consisted of a grid of 25 perches: 21 perches were simple perches and 4 of 9 central perches had the thick woody structure.

Plot visitation

In winter 1998–1999, each study site was visited twice a month from October through March (12 visits). In winter 1999–2000, each study site was visited once in September, twice a month from October through January, and once in March (10 visits). Each plot was observed twice on each visit: once in the morning and once in the afternoon. While the sequence of plot visitation was randomized among visits, the morning and afternoon sequences remained consistent within a visit to avoid a crepuscular bias. Observations were made from a truck parked at a distance of at least 50 m from the plot to minimize observer-induced changes in bird behavior such as leaving the plot or moving to a perch further away from the observation vehicle.

Raptor behavioral observations

We used 10 × 40 binoculars and 15 × 60 to 60 × 60 zoom spotting scopes to determine the instantaneous abundance of all raptors; measurements were taken four times at 5-min intervals (0, 5, 10, and 15 min). We noted the number of raptors on each plot and all movements, including entering, leaving, and moving between perches within a plot. We also noted the total amount of time that each site was occupied by an individual of the focal species during each observation period. When more than one individual of a species used a plot, times for all individuals were combined for analysis. American Kestrels were identified as either male or female on the basis of plumage, while Northern Harriers were categorized as adult males or birds with brown plumage; the sexes of observed Loggerhead Shrikes could not be determined on the basis of visual cues and were not recorded.

Vegetation data

At each study plot, we collected data on vegetation from five points, one near each corner and one in the center of the plot. At each point we measured vertical obstruction (Robel et al. 1970) and vegetation coverage (Daubenmire 1959).

Percent vertical obstruction was measured at heights of 25, 50, 75, 100, and 125 cm at 5 m north and south of the center of the plot. Percent coverage of a 0.2-m Daubenmire frame was measured for the following categories: bare ground, grass, forb, woody plants, standing water, and organic debris.

Statistical analyses

We measured plot use by examining species presence during a survey (occurrence). We used presence–absence data to test differences in plot use versus availability. To derive a measure of expected plot use to test against the observed plot use, we totaled, for each year, the number of times a species was observed on any type of plot and divided this total by the number of plot types. To test the hypothesis that species use plots in accordance with plot availability, we used a goodness-of-fit test (Sokal and Rohlf 1995). For instances where expected observations were less than five, we performed bootstrap procedures on 2000 iterations to ensure that small sample size did not affect test results.

We measured plot quality by examining time spent on a plot during a survey (duration). Both occurrence and duration were calculated after combining the morning and afternoon observations for each visit to avoid pseudo-replication. We standardized plot use with the following formula to reduce variability between species:

$$[1] \quad \sqrt{(T/30)} \times 100$$

where T is the time spent on a plot during one visit (two plot observations), and 30 is the maximum amount of time one individual may spend on a plot. The fraction $T/30$ was then converted to a whole number, and calculation of the square root created a scale of 0–10, weighting observation in favor of individuals using plots intermittently. We used a repeated measures ANOVA (RMANOVA) to determine differences in plot quality (duration) for American Kestrels, Loggerhead Shrikes, and Northern Harriers for each plot type (Sokal and Rohlf 1995). RMANOVA was also used as an omnibus test to examine plot use by visit. We used Tukey's mean separation tests to quantify differences in plot quality using MINITAB (Minitab Inc. 1998).

To measure the direct influence of interspecific interactions we used Pearson's product moment correlation to measure the association between the number of plots occupied by Loggerhead Shrikes and the number of plots occupied by each of the larger species. We measured species association with a species association test (Ludwig and Reynolds 1988), which is a 2 × 2 frequency table. The species association test provides only a direction (positive or negative) and the strength (χ^2 value) of an association, not the extent of overlap. We used Jaccard's overlap index to measure the extent of overlap (between 0 and 1) in plot usage as described in Ludwig and Reynolds (1988).

Finally, to test for homogeneity between study sites, we performed a two-way ANOVA by site and plot type for all of the following variables: vertical obstruction at heights of 25, 50, 75, and 100 cm; percent cover by category (bare ground, grass, forb, woody vegetation, and organic debris); and presence of water on the plot. Four plots on Matagorda Island were burned prior to vegetation measurements; therefore, we

eliminated these plots from the vegetation analysis. Since none of our variables displayed a site \times plot type interaction based on vegetation variables, we used a one-way ANOVA for a more conservative test of between-site differences.

Results

We monitored each plot for 360 min (12 visits) and 300 min (10 visits) in 1999 and 2000, respectively. Raptor assemblages and patterns of plot usage within species were similar at both study sites. The dominant species were Loggerhead Shrikes (by duration) and Northern Harriers (by presence) on Matagorda Island and American Kestrels (both duration and presence) at Norias (Tables 1 and 2). Female American Kestrels used manipulated plots almost exclusively despite the presence of both sexes at each site during each year. In addition to the three focal species, 10 other raptor species spent at least 1 min on at least one plot. Of these 10 species, White-tailed Kites (*Elanus leucurus*) and White-tailed Hawks (*Buteo albicaudatus*) used plots at both study sites irregularly, while Aplomado Falcons (*Falco femoralis*), Crested Caracaras (*Caracara plancus*), Merlins (*Falco columbarius*), and Peregrine Falcons (*Falco peregrinus*) used Matagorda Island plots intermittently.

Since no interaction terms were significant, we used one-way ANOVAs for our vegetation comparisons between study sites. Based on the vegetation variables, plots at Norias had greater amounts of bare ground and vertical obstruction between 75 and 100 cm than plots on Matagorda Island ($F_{[1,34]} = 11.6$, $P < 0.01$, for bare ground coverage; $F_{[1,34]} = 14.26$, $P < 0.01$, for vertical obstruction between 75 and 100 cm). Plots at Norias had lower amounts of vertical obstruction between 0 and 25 cm and less ground coverage categorized as forb or organic debris than plots on Matagorda Island ($F_{[1,34]} = 12.0$, $P < 0.01$, for vertical obstruction at 0–25 cm; $F_{[1,34]} = 9.44$, $P < 0.01$, for forb coverage; $F_{[1,34]} = 21.31$, $P < 0.01$, for organic debris coverage). Owing to differences in plot vegetation and plot use by raptor species, we analyzed study sites separately.

Perch use by species

As expected, American Kestrels and Loggerhead Shrikes did not use plot types equally at either site during winter 1998–1999 ($\chi^2_4 = 10.74$ and 27.91 , $P < 0.01$, for Loggerhead Shrikes at both sites; $\chi^2_4 = 30.54$ and 15.04 , $P < 0.01$, for American Kestrels at both sites) (Tables 1 and 2). Equable plot use by Northern Harriers validated our prediction that these birds are not perch limited. In the winter of 2000, we eliminated the open control plots, and all species used plots in accordance with plot availability. For Loggerhead Shrikes, there was no evidence of plot selection at either site ($\chi^2_2 = 3.36$, $P = 0.18$, for Matagorda Island; $\chi^2_2 = 1.0$, $P = 0.59$, for Norias), but American Kestrels at Norias preferred artificial perches to natural woody structure ($\chi^2_2 = 2.23$, $P = 0.33$, for Matagorda Island; $\chi^2_2 = 5.25$, $P = 0.07$, for Norias). When open controls are eliminated from the 1998–1999 analyses, three of four relationships remained significant (Loggerhead Shrikes: $\chi^2_3 = 15.35$, $P < 0.01$, for Matagorda Island; $\chi^2_3 = 4.79$, $P = 0.18$, for Norias; American Kestrels: $\chi^2_3 = 10.26$, $P = 0.02$, for Matagorda Island; $\chi^2_3 = 7.77$, $P = 0.05$, for Norias).

Perch quality

There were significant differences in duration of plot use by plot type ($F_{[4,540]} = 8.86$, $P < 0.001$, for Matagorda Island; $F_{[4,540]} = 25.78$, $P < 0.001$, for Norias), species ($F_{[2,540]} = 4.50$, $P < 0.011$, for Matagorda Island; $F_{[2,540]} = 168.82$, $P < 0.011$, for Norias), and the interaction between plot type and species ($F_{[8,540]} = 16.30$, $P < 0.001$, for Matagorda Island; $F_{[8,540]} = 23.45$, $P < 0.001$, for Norias) for both sites during winter 1999. The repeated measure, visitation date, was not significant, but the species \times visitation (plot type) interaction term was significant ($F_{[110,540]} = 1.27$, $P = 0.047$) in 1999 for Matagorda Island. Tukey's mean separation tests on the plot \times species interactions showed that American Kestrels at Norias used manipulations significantly more than they used controls ($T_4 = 8.2$ – 13.3 , $P < 0.01$, for all comparisons), but American Kestrels displayed no preference for perch height ($T_4 = 0.52$ – 2.26 , $P > 0.25$, for all comparisons). Use of woody controls by Loggerhead Shrikes was significantly greater than other plot-species combinations on Matagorda Island ($T_4 = 4.5$ – 9.7 , $P < 0.01$, for all comparisons). At Norias, use of plots by American Kestrels was nearly 10 times that of Loggerhead Shrikes or Northern Harriers, while on Matagorda Island, use of woody controls (by duration) by Loggerhead Shrikes was more than twofold greater than that of American Kestrels, the next most common species.

Similar plot duration patterns were observed during winter 2000 (Table 2). For Matagorda Island only, the species \times plot interaction term proved significant ($F_{[4,270]} = 3.55$, $P < 0.01$), with the differences due to increased use of woody controls by Loggerhead Shrikes compared with American Kestrels (Tukey's mean standard test, $T_2 = 3.264$, corrected $P = 0.03$). At Norias, all terms and interactions except visitation date were significant (plot type, $F_{[2,270]} = 8.09$, $P < 0.001$; species, $F_{[2,270]} = 55.47$, $P < 0.001$; species by plot type, $F_{[4,270]} = 7.96$, $P < 0.01$; species by date within plot type, $F_{[54,270]} = 1.81$, $P < 0.01$). Tukey's mean separation test showed that use of manipulations by American Kestrels drove both the observed plot type differences and the species \times plot type interactions ($T_2 = 5.4$ – 8.7 , corrected $P < 0.01$, for all differences in patch use both among species and intraspecifically for American Kestrels).

Interspecific interactions

The number of plots used by Loggerhead Shrikes was, in general, negatively correlated with the number of plots occupied by larger species. Northern Harriers clearly had a much stronger impact than American Kestrels (Table 3). The species association tests showed that Loggerhead Shrikes and American Kestrels were negatively associated at both sites, but the association was significant only at Norias (Table 4). The limited number of occurrences of both Loggerhead Shrikes and Northern Harriers precluded significant associations between these species at either site owing to low power (Table 4). For Loggerhead Shrikes, the average number of plots used decreased after the first 2 weeks in November in both years for all plot types except woody controls (Fig. 1). The decrease in plot use by Loggerhead Shrikes was coupled with an increase in plot use by Northern Harriers at both sites in both years (Fig. 1).

Table 1. Plot use by Loggerhead Shrikes (*Lanius ludovicianus*), American Kestrels (*Falco sparverius*), and Northern Harriers (*Circus cyaneus*) in winter 1998–1999.

	Number of visits to plots												Time (min; mean ± SE) spent on plot ^a						
	Tall			Short			Mix			Open			Woody			All plot types			
	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp	Tall	Short	Mix	Open	Woody	All plot types	Total time
Norias 1999																			
Loggerhead Shrike	3	3.8	2	3.8	6	3.8	0	3.8	8	3.8	3.8	19	0.54±0.06	0.13±0.02	1.21±0.10	0.00±0.00	2.79±0.15	0.93±0.02	224
American Kestrel	34	26	35	26	38	26	5	26	18	26	26	130	12.27±0.24	10.90±0.20	14.08±0.22	0.33±0.03	1.75±0.08	7.87±0.04	1888
Northern Harrier	6	8.2	12	8.2	9	8.2	6	8.2	8	8.2	8.2	41	0.29±0.02	0.79±0.04	0.81±0.05	0.33±0.02	0.15±0.01	0.48±0.01	114
Matagorda Island 1999																			
Loggerhead Shrike	7	9.2	11	9.2	5	9.2	1	9.2	22	9.2	9.2	46	0.77±0.04	1.83±0.09	0.42±0.03	0.06±0.01	5.65±0.18	1.75±0.02	419
American Kestrel	10	4.6	3	4.6	8	4.6	1	4.6	1	4.6	4.6	23	3.33±0.13	0.48±0.05	2.13±0.12	0.02±0.00	0.00±0.00	1.16±0.02	286
Northern Harrier	23	17.4	15	17.4	19	17.4	16	17.4	14	17.4	17.4	87	1.40±0.04	0.83±0.04	0.92±0.03	0.65±0.02	0.54±0.03	0.87±0.01	209

Note: Obs, observed; Exp, expected. Tall, short, and mix refer to perch height on plots. Open and woody refer to control plots. All plots had four replicates and were therefore equal in availability. American Kestrels favored plots with manipulations, while Loggerhead Shrikes favored woody control plots on Matagorda Island.

^aTime spent on plot refers to an individual plot during one census period of 30 min (*n* = 48).

^bAverage time for all plot types was based on 240 observations made in 1998–1999.

Table 2. Plot use by Loggerhead Shrikes, American Kestrels, and Northern Harriers in winter 1999–2000.

	Number of visits to plots						All plot types	Time (min; mean ± SE) spent on plot ^a				Total time
	Brushy		Regular		Woody			Brushy	Regular	Woody	All plot types ^b	
	Obs	Exp	Obs	Exp	Obs	Exp						
Norias 2000												
Loggerhead Shrike	6	8.3	10	8.3	9	8.3	25	1.70±0.11	3.10±0.15	2.50±0.12	2.43±0.04	292
American Kestrel	30	24.7	27	27.7	15	24.7	72	10.78±0.23	10.40±0.25	3.13±0.17	8.10±0.08	972
Northern Harrier	9	7	6	7	6	7	21	1.20±0.89	0.35±0.03	0.28±0.02	0.61±0.02	73
Matagorda Island 2000												
Loggerhead Shrike	7	7.3	4	7.3	11	7.3	22	1.60±0.11	0.43±0.04	2.80±0.16	1.61±0.04	193
American Kestrel	6	5.7	8	5.7	3	5.7	17	2.13±0.15	1.78±0.11	0.20±0.02	1.37±0.04	164
Northern Harrier	14	11.7	12	11.7	9	11.7	35	0.65±0.02	0.88±0.06	0.38±0.02	0.63±0.04	76

Note: Obs, observed; Exp, expected. Brushy and regular refer to canopy type of perches on plots. Woody refers to control plots with natural woody vegetation. All plots had four replicates and were therefore equal in availability. Plot use followed availability in winter 2000 for all species.

^aTime spent on plot refers to an individual plot during one census period of 30 min (*n* = 40).

^bAverage time for all plot types was based on 120 observations made in 1999–2000.

Table 3. Effects of larger raptor species on Loggerhead Shrikes from Norias and Matagorda Island.

Species	Site	1999			2000		
		<i>r</i>	<i>n</i>	<i>P</i>	<i>r</i>	<i>n</i>	<i>P</i>
Northern Harriers	Norias	−0.683	12	0.015	−0.604	10	0.064
	Matagorda Island	−0.521	12	0.083	−0.296	10	0.405
American Kestrels	Norias	−0.055	12	0.466	−0.095	10	0.793
	Matagorda Island	−0.345	12	0.273	−0.371	10	0.290

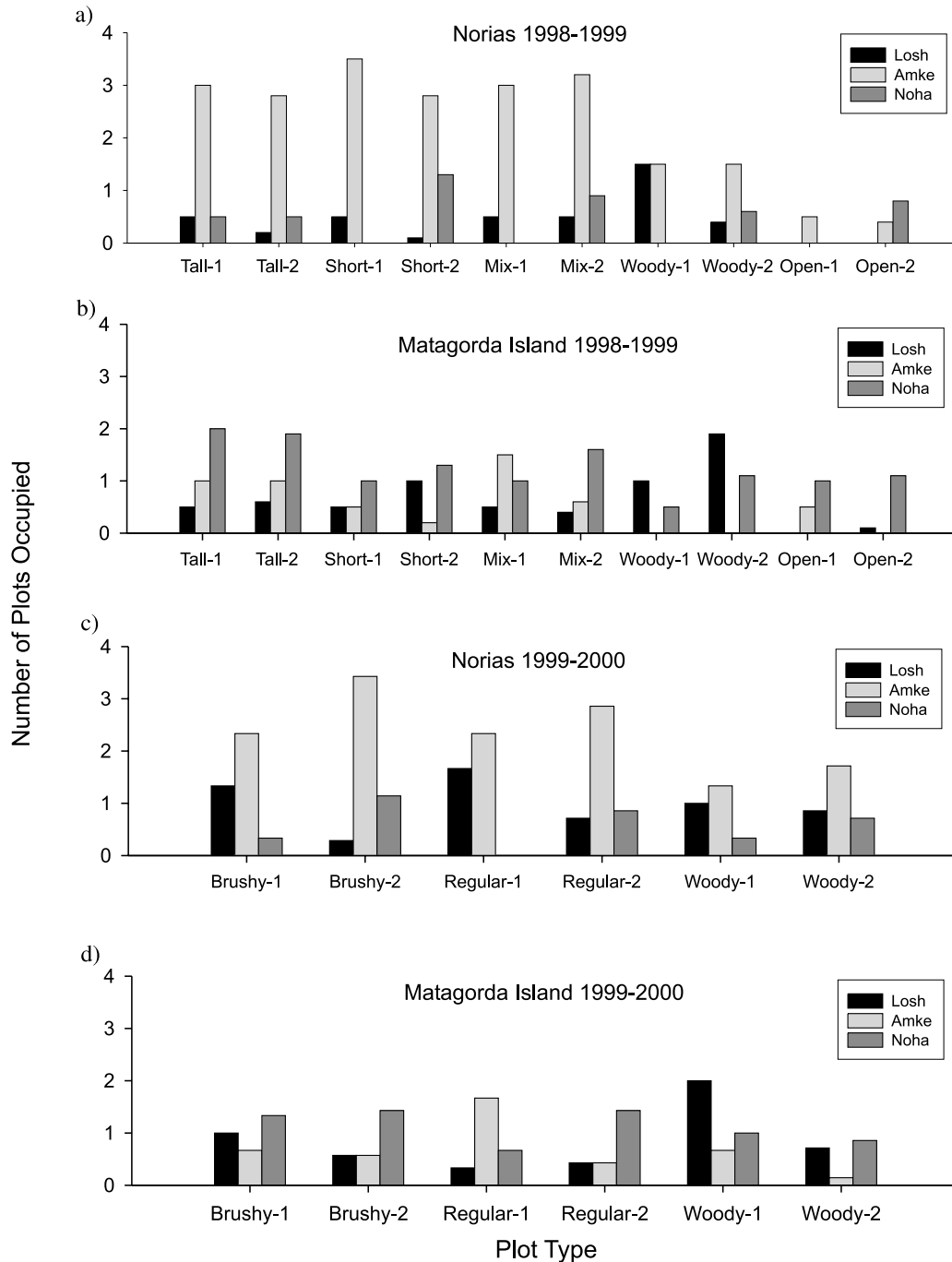
Note: *r* is the correlation coefficient between number of plots used by Loggerhead Shrikes and number of plots used by the two larger species. Sample size is based on number of visits made to each site throughout the year. In three of the four analyses of Northern Harriers and Loggerhead Shrikes, negative correlation coefficients below −0.5 were observed, implying that Northern Harrier densities negatively affect Loggerhead Shrike densities.

Table 4. Species association tests by site and year.

Species pairs	Sign	χ^2	<i>P</i>	JO
Norias 1999				
Loggerhead Shrike – American Kestrel	–	6.40	0.02	0.02
Loggerhead Shrike – Northern Harrier	–	0.06	0.25	0.02
American Kestrel – Northern Harrier	–	0.91	0.25	0.02
Matagorda Island 1999				
Loggerhead Shrike – American Kestrel	–	1.80	0.20	0.01
Loggerhead Shrike – Northern Harrier	–	0.69	0.25	0.06
American Kestrel – Northern Harrier	–	0.13	0.25	0.05
Norias 2000				
Loggerhead Shrike – American Kestrel	–	6.0	0.02	0.19
Loggerhead Shrike – Northern Harrier	–	1.5	0.20	0.19
American Kestrel – Northern Harrier	+	1.7	0.20	0.12
Matagorda Island 2000				
Loggerhead Shrike – American Kestrel	–	0.76	0.25	0.02
Loggerhead Shrike – Northern Harrier	–	0.55	0.25	0.02
American Kestrel – Northern Harrier	+	1.94	0.20	0.02

Note: Sign indicates whether the association is positive or negative. Bold values indicate significance at *P* < 0.05. JO refers to Jaccard’s overlap index; numbers may vary from 0.0–1.0. The only significant association was between American Kestrels and Loggerhead Shrikes at Norias. Lack of association between Loggerhead Shrikes and Northern Harriers is due to minimal plot occupancy by both species, despite equal or greater overlap between Loggerhead Shrikes and Northern Harriers compared with Loggerhead Shrikes and American Kestrels.

Fig. 1. Patch use measured as mean number of plots occupied by species (American Kestrels (Amke), *Falco sparverius*; Northern Harriers (Noha), *Circus cyaneus*; Loggerhead Shrikes (Losh), *Lanius ludovicianus*). For definitions of plot types, see text. The numeral following plot type indicates either (1) average plot use prior to 1 November or (2) average plot use after 1 November when wintering Northern Harrier numbers stabilize. (a) Norias winter 1998–1999, (b) Matagorda Island winter 1998–1999, (c) Norias winter 1999–2000, (d) Matagorda Island winter 1999–2000. As the winter progressed, Loggerhead Shrike abundance generally decreased while Northern Harrier abundance increased. Plot use by Loggerhead Shrikes is limited by Northern Harrier plot use in the absence of escape cover (woody control); this is evident during winter 1998–1999 and at Norias during winter 1999–2000.



Discussion

Perch limitation

As expected, Loggerhead Shrikes and American Kestrels used areas with woody structure more than areas without woody structure, while Northern Harriers displayed no pref-

erence for any type of plot. When open controls were removed (winter 1999–2000), American Kestrels were the only species that showed a plot preference by occurrence (preferring artificial perches to natural woody vegetation), and then only at Norias. Elimination of the open controls from the data for the first year resulted in a similar pattern;

that is, American Kestrels preferred artificial perches. The preference of American Kestrels for plots with perches (both natural and artificial) implies that perch limitation exists for this species, while the preference of Loggerhead Shrikes for natural perches implies that interspecific interactions may have been driving plot use patterns by this species.

The open landscapes used for this study produced a female-biased sex ratio in wintering American Kestrel populations (Table 1), implying that such habitat is of superior quality for either foraging (Smallwood 1987, 1988; Bird 1988) or predator avoidance (Ardia and Bildstein 1997). American Kestrels displayed a preference for manipulations over woody controls at both sites in both years, yet there was no evidence that either Loggerhead Shrikes or American Kestrels used tall manipulations more than short manipulations.

Plot quality

While results based on occurrence by plot type were equivocal, patterns of plot use by duration were strong and significant. At both study areas, American Kestrels spent the majority of their time on manipulated plots, while Loggerhead Shrikes preferred woody controls. In addition, time on plot varied by study site much more for American Kestrels than for Loggerhead Shrikes (Table 1 and Fig. 1). As the majority of prey captures by both American Kestrels and Loggerhead Shrikes were ground strikes from elevated perches, the increased ground cover on Matagorda Island may have affected larger American Kestrels to a greater extent than smaller Loggerhead Shrikes. Plot type preference has a predator avoidance component for both species, but selective forces are different for Loggerhead Shrikes and American Kestrels. Again, owing to their smaller size, Loggerhead Shrikes may utilize the complex canopies of mesquite, yaupon holly (*Ilex vomitoria*), and live oak as escape cover. Thick, wooded stands are generally avoided by American Kestrels as these stands may allow accipiters (especially Cooper's Hawks, *Accipiter cooperii*) to approach undetected (Ardia and Bildstein 1997). These stands serve as a refuge for Loggerhead Shrikes but may predispose American Kestrels to predation. Finally, ground cover below perches may be more important than perch height in determining American Kestrel perch quality (Smallwood 1988; Gawlik and Bildstein 1993).

Interspecific associations

The only significant species association was between Loggerhead Shrikes and American Kestrels at Norias (Table 4), where the presence of American Kestrels interfered with plot use by Loggerhead Shrikes. Interference by the larger species is consistent with the ideal despotic distribution of Fretwell and Lucas (1970), where the larger species has a competitive advantage, usurping the resource from the smaller species. When American Kestrels were not present in large numbers (e.g., during winter 1999 on Matagorda Island), plot use by Loggerhead Shrikes increased. While the Loggerhead Shrike – American Kestrel species association statistics were not significant on Matagorda Island for either year, Jaccard's overlap index values were lower on Matagorda Island than at Norias each year, implying less overlap on Matagorda Island. We believe the small sample size associated with both Loggerhead Shrikes and Northern

Harriers resulted in insufficient power to detect a significant negative association between these two species (Table 4). American Kestrel preference for manipulations generally restricted Loggerhead Shrikes to areas that provided escape cover, such as woody controls and brushy manipulations.

The species association pattern displayed at Norias in 2000 was not consistent with American Kestrels preying on Loggerhead Shrikes (Table 4) as there was a 20% overlap in habitat use by these species. Loggerhead Shrikes moved, often off of a plot, because of the presence of American Kestrels, but usually remained visible, often returning to a plot if the American Kestrel left during the observation period. Such limited overlap may be attributed to either competitive exclusion by the American Kestrel or a shift in plot use by Loggerhead Shrikes from perches with a simple canopy favored by a superior competitor to defensible perches that double as refuges (Williams and Batzli 1979; Korpimäki 1987). For example, of the 11 instances where both Loggerhead Shrikes and American Kestrels co-occurred on plots, there were seven interactions that ended with the larger American Kestrel driving the smaller Loggerhead Shrike away from the plot, indicating interspecific competition (Jaksic 1985).

While American Kestrels appeared to interfere with plot use by Loggerhead Shrikes, Northern Harriers prevented Loggerhead Shrikes from using plots without escape cover. Sih et al. (1985) and Hakkarainen and Korpimäki (1996) stressed the importance of predation in shaping and regulating species assemblages, and while use of plots by Northern Harriers at both study sites during both years did not deviate from plot availability, Loggerhead Shrike use (duration) of plots was skewed in favor of plots with perches doubling as refuges. Northern Harrier densities at Norias were approximately half those on Matagorda Island, suggesting that Northern Harrier pressure on Loggerhead Shrikes may have been reduced at Norias. Jaccard's overlap index showed a similar pattern of little overlap between Loggerhead Shrikes and Northern Harriers, except at Norias in 2000 (Table 4). These Jaccard's overlap index values were inflated because Northern Harrier numbers were low; therefore, instances where Loggerhead Shrikes and Northern Harriers overlapped on woody control plots resulted in a disproportionate impact on the overlap index values (Hubalek 1982). There were seven instances where Northern Harriers flew in or near a plot occupied by Loggerhead Shrikes; in each instance, the Loggerhead Shrike flew directly to cover, often remaining within thick brush until the end of the observation period (at least 10 min).

Time spent on a plot (duration) by Loggerhead Shrikes at Norias may have been influenced by interference competition from American Kestrels, but it could also have been influenced by differences in patch choice (plot use) resulting from Northern Harrier predation pressure. We draw these inferences based on changes in plot usage prior to, and after, 1 November each year (Fig. 1). By this date, most wintering Northern Harriers are at the study sites (D.H. Kim, unpublished data) and appear to affect plot selection by Loggerhead Shrikes but not by American Kestrels. To optimize fitness, many small birds and mammals must choose between exposed high-quality patches and lower quality patches offering refuge from predation. For example, re-

sources being equal, both White-crowned Sparrows (*Zonotrichia leucophrys*) and House Sparrows (*Passer domesticus*) utilized areas providing refuge from predators instead of foraging in the open (Grubb and Greenwald 1982). Crested Tits (*Parus cristatus*) foraging in mature and sapling forest patches switched from upper canopy to lower canopy in response to changes in predation risk associated with foraging position (Krams 1996). We believe that predation risks for Loggerhead Shrikes forced them away from open areas to areas that provided similar energy returns as well as refuge from predation. Furthermore, release from predation pressure during the early part of winter 2000 allowed Loggerhead Shrikes to use all suitable hunting stations in proportion to their availability at Norias.

Loggerhead Shrikes occupy a unique niche in this species assemblage because although they are clearly predators, their diminutive size subjects them to potential predation from all other raptor species in the study areas. As an upper trophic level species, Loggerhead Shrikes should be limited by competition (Hairston et al. 1960); therefore, Loggerhead Shrike abundance should be limited by competitive interactions with larger species (Schoener 1983). As expected, larger species do affect plot usage by Loggerhead Shrikes, but not only through competition. Northern Harriers and other raptors exclude Loggerhead Shrikes by their mere presence, while the slightly larger American Kestrels usurp plots that may have otherwise been used by Loggerhead Shrikes. The results of the RMANOVA analysis had significant three-way interaction terms but they also showed that the plot \times species interactions were important, implying that American Kestrels spend large amounts of time on manipulations, while Loggerhead Shrikes spend more time on woody controls, avoiding both predation and competition.

Finally, patterns of plot usage by the focal species and differences in plot vegetation between Norias and Matagorda Island may be due to a difference in the landscape context between sites. Matagorda Island is grassland with patches of woody vegetation, while Norias is mesquite-oak woodland with a strip of coastal prairie as buffer between the Laguna Madre and the forest. Forest edge and oak mottes at Norias provide superior roosting habitat for American Kestrels, resulting in an increase in the overall number of American Kestrels at Norias. The presence of thicker woody vegetation and fragmented grassland patches may also increase American Kestrel abundance while restricting Northern Harrier abundance.

Prescribed burns are used on Matagorda Island to prevent woody encroachment and maintain grassland integrity. At Norias, grazing is the main disturbance, although fire is used to control brush and improve the nutrient content of native grasses for grazing cattle. Grazing results in changes to ground cover such as reduced vertical obstruction near the ground and more exposed bare ground, which (according to other studies) enhances American Kestrel habitat at the patch scale and results in a female-biased sex ratio (Smallwood 1987; Gawlik and Bildstein 1995). The Matagorda Island study plots, and Matagorda Island grasslands in general, have denser grass and forb cover (as indicated by higher vertical obstruction values within the first 25 cm) and less bare ground compared with prairie patches at Norias.

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