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TERRITORY-SIZE REGULATION IN BLACK-SHOULDERED KITES

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ABSTRACT.—We studied the relationship of Black-shouldered Kite (*Elanus caeruleus*) territory size to prey abundance and competitor abundance in northwestern California. Kite territory size ranged from 1.6 to 21.5 ha (n = 26). The estimated mean number of California voles (*Microtus californicus*) per territory was 1,483 ± SE of 163 (n = 25). Competitor abundance (i.e. total raptor abundance) ranged from 4.8 to 31.0 individuals/km^2 and was strongly correlated with abundance of *M. californicus.* Both estimated prey abundance and competitor abundance were inversely correlated with kite territory size. After developing multiple-regression models using both variables, partial-correlation analysis revealed that once the effects of prey abundance were statistically controlled, competitor abundance continued to be significantly correlated with kite territory size. When the effects of competitor abundance were statistically controlled, prey abundance was no longer significantly correlated with kite territory size. In that it appears that the number of competitors was a function of number of prey, we conclude that kite territory size is proximately regulated by competitor abundance and ultimately regulated by prey abundance. *Received 3 August 1992, accepted 14 March 1993.*

THE RELATIONSHIP BETWEEN raptors and their prey has been studied extensively (e.g. Craighead and Craighead 1956, Village 1982, 1987, 1989, Korpimäki 1984, 1985a, b, 1988, Newton et al. 1986). Most raptor-prey studies have focused either on raptor abundance (Baker and Brooks 1981, Village 1982, Cully 1991) or raptor reproductive success (Hammerstrom 1979, Smith et al. 1981, Korpimäki 1986, 1988, Ridpath and Brooker 1986) in relation to prey abundance. Few studies have examined the relationship between raptor territory size and prey abundance (for exceptions, see Village 1982, 1987, Temeles 1987), probably because of the difficulty of measuring territory size of wide-ranging birds, and in estimating abundance of several types of prey (e.g. rodents, rabbits, and birds) over those relatively large areas.

Generally, theory predicts that territory size should be inversely related to food abundance (for exceptions, see Schoener 1983, 1987, Ebersole 1980). Myers et al. (1979) presented two hypotheses regarding territory-size regulation. First, individuals establish territories of a size that contains adequate resources to meet their energetic needs. Second, an individual will defend as large an area as it can, constrained by competition with other individuals. These hypotheses are not mutually exclusive, although they have generally been viewed as such (Myers et al. 1979).

We studied the relationship of the size of Black-shouldered Kite (*Elanus caeruleus*) hunting territories to prey abundance and competitor abundance. Kites are good subjects for such a study because: (1) they have distinctive hunting habits (hovering), which allows unambiguous descriptions of areas/points used for foraging; (2) they use open to semiopen habitats, facilitating long, continuous observation periods; (3) they are at the top of the food chain, so their territory size is not likely to be influenced by predation; (4) they have relatively small home ranges or territories compared with other raptors (Henry 1983); and (5) they rely almost exclusively on rodents as prey (Waian and Stendell 1970), primarily California voles (*Microtus californicus*) in California (Stendell 1972, Bammann 1975). Thus, estimating kite prey abundance is an easier task than it would be with a more generalist predator.

METHODS

The study was conducted on the Fay Slough Wildlife Area in Eureka, California. The 135-ha area was used for cattle grazing prior to 1987 when it was acquired by the California Department of Fish and Game. It is composed primarily of ungrazed pasture with small patches of alders (*Alnus* spp.) and blackberry bushes (*Rubus* spp.). Alders were planted along slough borders in 1988, providing important perching locations for raptors. A number of freshwater and

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brackish sloughs dissect the area. The topography is flat with elevations ranging from −0.5 m to 2 m. The climate in the area is maritime, with cool summers and mild winters. Summers are characterized by foggy nights and mornings. Precipitation was greatest between November and April though some rain occurred during most months of this study. The growing season is generally between April and July, when grasses develop, then drop their seeds. Vegetation composition and structure were relatively constant throughout the study, although limited (rotational) grazing occurred on approximately 35 ha beginning in December 1989. Primary plant species included Italian ryegrass (*Lolium multiflorum*), perennial ryegrass (*L. perenne*), velvet grass (*Holcus lanatus*), and buttercups (*Ranunculus* spp.).

Kites were captured with a selective pole trap (Dunk 1991), then banded with uniquely colored leg bands. Kite hunting territories were estimated from June 1989 through November 1990. Each territory was delineated by observing a kite and documenting all locations where the bird hovered, perched, or interacted with another kite or some other raptor. Locations were estimated by measuring distance with an optical range finder and direction with a compass from fixed observation spots. The accuracy of the range finder was ±1% at 100 m and ±10% at 1,000 m. For each location, distance, direction, and time (to the nearest 0.05 min) were recorded on a microcassette recorder. Each kite was observed for a minimum of 1.5 h or until the bird left the area to roost. Total observation time per territory ranged from 1.5 to 12.25 h over a one- to seven-day period. Mean number of locations per territory was 64.5 ± SD of 24.2. Adequacy of sampling hunting territories was determined graphically by plotting hunting territory size and number of locations until reaching an asymptote. Hunting territory size was estimated using the 95%-minimum-convex-polygon estimator in program HOME RANGE (Ackerman et al. 1989).

We attempted to delineate as many hunting territories as possible. We did not randomly choose individuals to observe, but selected individuals according to the following priority: (1) color-banded birds with a territory not previously measured; (2) previously unmeasured territories of unbanded individuals that were repeatedly associated with a specific geographic area prior to the sampling time; and (3) color-banded individuals whose territories had been previously estimated. Unbanded birds were identified using one or more of the following criteria: (1) unique molting patterns; (2) perches used; (3) association with (i.e. mates of) banded kites; and (4) age (i.e. whether adult or juvenile).

We sampled vegetation structure and composition within two weeks of delineating each hunting territory. After plotting territory boundaries on a 1:2,400 aerial photograph, 100 vegetation plots were established in a random systematic design for each territory in order to have complete coverage of the territory. In each plot, we measured the percentage of the plot covered by: (1) green grass (Gramineae); (2) brown grass; (3) green herbaceous vegetation; (4) brown herbaceous vegetation; (5) seed heads on grasses; (6) green rush (Cyperaceae); and (7) brown rush. Variables 6 and 7 were estimated beginning in December 1990. These seven variables were estimated by eye and placed into one of six cover classes: 0%, 1–20%, 21–40%, 41–60%, 61–80%, and 81–100%. Cover height, an estimate of the height at which there was 100% cover horizontally, also was measured in the center of each plot by pushing a meter stick through the vegetation, flush to the ground, and recording the height (cm) of the intersection between plot center and the meter stick. Plots falling on flooded areas were classified as flooded with no vegetation characteristics estimated within them.

Potential competitors of kites (other vole-eating raptors) were counted once each month within 14 days of estimating each territory. From a central location, we counted the numbers of each raptor species by scanning the entire study area (approximately 95% of the area could be viewed). Counts were terminated when three consecutive counts yielded identical results. All counts were made within 1 h of sunset because previous observations showed that this was the period of greatest raptor activity. Common Barn-Owls (*Tyto alba*) were counted by looking in the two barns on the study area.

Microtus californicus were trapped monthly within four randomly located permanent trapping grids. Grids consisted of 40 traps spaced 5 m apart and arranged in an 8 × 5 pattern. Traps were locked open for 24 to 36 h prior to being set each month. Before being set, traps were baited with bird seed and polyester pillow stuffing was added. Traps were checked just after first light and just before dark for four consecutive days. Because there was no evidence from our study to suggest that *M. californicus* activity differed between day and night, we did not distinguish between day and night captures. At each capture location, individuals were uniquely toe-clipped, weighed (g), sexed, and released (for more detailed description of small-mammal trapping, see Dunk 1992). Vole densities within grids were estimated by dividing number of individuals caught by grid area. Within one week of trapping, vegetation was sampled in each trapping grid. Vegetation plots were placed within 0.5 m of each trap, and the same parameters were estimated as in kite hunting territories.

To estimate vole abundance within each kite territory, we categorized each vegetation plot within a territory as being of high-, medium-, or low-quality habitat for voles. This was done after modelling vole-vegetation associations using stepwise discriminant analysis each month (see Dunk 1992). This procedure was effective at predicting vole abundance (mean correct classification = 70.03% ± SE of 2.66). Vegetation

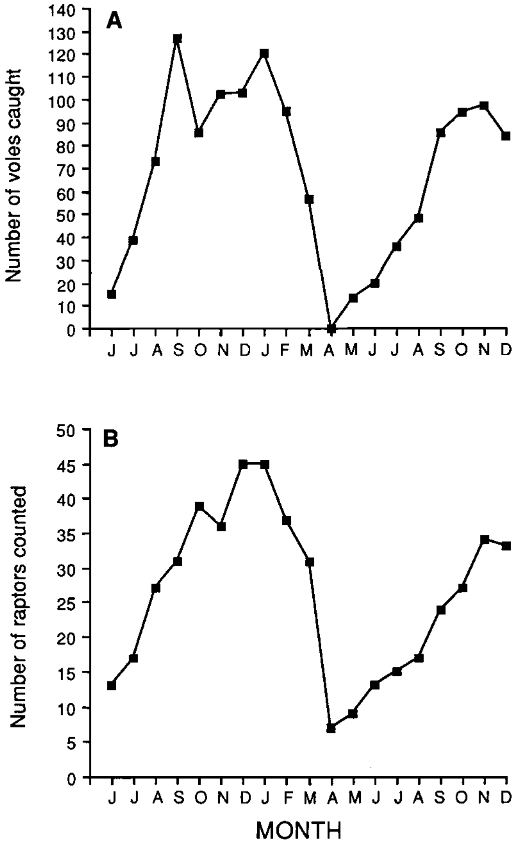

Fig. 1. (A) Number of *Microtus californicus* caught and (B) number of raptors counted each month on Fay Slough Wildlife Area (June 1989–December 1990).

plots from kite territories were classified using the discriminant model developed closest to the time the territory was delineated. Generally, vole populations increased when seeds fell from grasses and became available to them. Vole populations were larger in areas with lower cover height and larger percentage brown grass cover (Dunk 1992). High-, medium-, and low-quality vole habitat was defined relative to the largest number of individuals caught within a month. The percentage of plots in each habitat-quality category was multiplied by territory area, then by naive density (number of individuals caught/grid area) of voles for that category. These were added together to estimate vole abundance for each territory.

Three methods of relating kite territory size to vole abundance were used: (1) regressing territory size on a monthly index of vole abundance expressed as number of individuals caught per 640 trap-nights for the four grids combined; (2) regressing territory size on the estimate of the number of voles within each territory; and (3) regressing territory size on the estimate of vole density within each territory. We also examined the effects of potential competitor abundance on kite territory size by regressing territory size on the estimate of competitor abundance for the month closest to the time the territory was delineated.

We used multiple-regression and partial-correlation analyses to evaluate simultaneously the effects of food abundance and competitor abundance on territory size. Partial-correlation analysis examines the effects of each independent variable while statistically controlling for the effects of variables already entered into the multiple-regression model (Neter et al. 1989); it allows for statistical controls when experimental controls are not feasible (Siegel and Castellan 1988). Partial correlation is useful for examining relationships among a dependent and two or more independent variables when there is a strong relationship between or among independent variables.

RESULTS

In all, 26 kite hunting territories were estimated; three individual's territories were estimated more than once. We were unable to sample vegetation within the territory of one kite. Territory size ranged from 1.6 to 21.5 ha ($\bar{x}$ = 7.8 ± SE of 1.0, n = 26). Vole populations fluctuated annually (Fig. 1A) with populations ranging from 0–914 individuals/ha. Mean estimated number of voles per kite territory was 1,483 ± 163 (n = 25). Vole density within kite territories ranged from 0 to 602/ha ($\bar{x}$ = 277.8 ± 33.2). Potential competitor abundance ranged from 7 to 45 individuals ($\bar{x}$ = 28.9 ± 5.7, n = 26), or 4.8 to 31.0 individuals per km^2 (Table 1).

The correlation between kite territory size and the estimate of prey abundance within each territory was not significant ($r = 0.23$, $P = 0.261$, $n = 25$). Kite territory size was negatively correlated with both total raptor abundance and the index of prey abundance ($r = -0.78$ and -0.75, respectively; $P < 0.001$ for both; Fig. 2). Territory size was also negatively correlated with the estimated density of voles within each territory ($r = -0.71$, $P < 0.001$, $n = 25$). A significant negative correlation also was found between territory size and abundance of conspecifics ($r = -0.64$, $P < 0.001$, $n = 26$). We found a significant correlation between total raptor abundance and the index of vole abundance each month (all grids combined; $r = 0.90$, $P < 0.001$, $n = 19$).

Because separate partial correlation analyses of each year's data (June 1989 through May 1990 and June 1990 through December 1990) showed similar results (Table 2), all data were combined

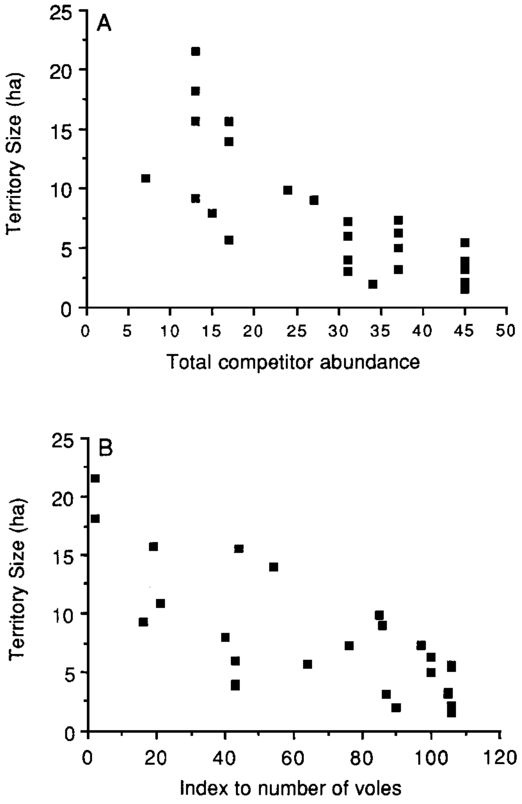

Fig. 2. Relationship of territory size (A) to competitor abundance and (B) to an index of numbers of *Microtus*.

for subsequent analyses. When regressing kite territory size on the estimate of vole density within kite territories and competitor abundance (total raptors), only competitor abundance was entered into the model ($r = -0.76$, $P < 0.001$, $n = 25$). Partial-correlation analysis revealed that once competitor abundance was controlled statistically, prey density did not explain a significant amount ($r = -0.25$, $P > 0.20$, $n = 25$) of the remaining variation in territory size (Table 3). When both variables were forced to enter the model, the partial correlation of competitor abundance remained significant ($r = -0.45$, $P < 0.05$, $n = 25$) when prey density was statistically controlled. Second, we regressed kite territory size on the estimate of prey density and kite abundance (conspecific competitors). Prey density was the only variable entered into the model ($r = -0.71$, $P < 0.001$, $n = 25$). When both variables were forced to enter the model (kite abundance was entered first), partial-correlation revealed prey density

TABLE 1. Monthly raptor counts at Fay Slough Wildlife Area, Eureka, California (June 1989–December 1990).

Species	Month																		
	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Black-shouldered Kite (*Elanus caeruleus*)	8	11	15	17	20	17	22	19	14	14	5	4	8	7	10	15	15	12	12
Red-tailed Hawk (*Buteo jamaicensis*)	2	2	3	3	3	2	3	3	3	3	1	2	2	3	2	2	2	3	2
Red-shouldered Hawk (*B. lineatus*)	1	1	2	2	3	3	2	3	1	1	0	2	1	2	2	2	2	3	2
Rough-legged Hawk (*B. lagopus*)	0	0	0	0	2	1	1	2	0	0	0	0	0	0	0	0	0	0	0
Northern Harrier (*Circus cyaneus*)	2	3	4	5	7	7	7	7	8	5	1	1	2	3	3	3	5	6	4
American Kestrel (*Falco sparvarius*)	0	0	2	3	3	2	4	4	4	3	0	0	0	0	0	1	2	3	3
Short-eared Owl (*Asio flammeus*)	0	0	0	0	0	3	5	6	6	4	0	0	0	0	0	0	0	6	8
Common Barn-Owl (*Tyto alba*)	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	1	2
Total	13	17	27	31	39	36	45	45	37	31	7	9	13	15	17	24	27	34	33

TABLE 2. Partial-correlation analysis results, by year, using Black-shouldered Kite territory size as dependent variable, and competitor abundance and prey abundance as independent variables.

Independent variables	r	Partial correlation	P for partial correlation	Adjusted r^2	Model P	n
		Year 1				
Competitor abundance	−0.875			0.748	<0.001	
Microtus density	−0.806	−0.339	0.20 < 0.10			
Competitor abundance	−0.875			0.748	<0.001	16
Index to numbers of *Microtus*	−0.775	−0.217	<0.50			
		Year 2				
Competitor abundance	−0.522			0.169	0.50 < 0.20	9
Microtus density	−0.495	0.003	<0.50			
Competitor abundance	−0.561			0.229	0.20 < 0.10	10
Index to numbers of *Microtus*	−0.532	−0.070	<0.50			

to continue to be significantly correlated with kite territory size ($r = -0.47$, $P < 0.05$, $n = 25$; Table 3). We also regressed kite territory size on the index of vole abundance and competitor abundance. Again, competitor abundance was the only variable entered into this model ($r = -0.780$, $P < 0.001$, $n = 26$). When both variables were forced into the model, partial correlation revealed that raptor abundance continued to be significantly correlated with kite territory size ($r = -0.446$, $P < 0.02$, n = 26, Table 3).

DISCUSSION

Three other investigators used partial correlation analyses to examine the relationships among food abundance, competitor abundance, and territory size of birds. Myers et al. (1979) found that, once the interaction between prey density and intruder (competitor) density was controlled statistically, prey density had no significant effect on territory size of Sanderlings (*Caladris alba*). Those findings are identical to ours when all raptors are considered as competitors. Conversely, McFarland (1986) found that food supply, not intruder pressure, determined territory size of New Holland Honeyeaters (*Phylidonyris novaehollandiae*). During the first year of his study, Temeles (1987) found that both mouse availability and intruder pressure explained some variation in territory size of Northern Harriers, $n = 7$ territories), whereas in the second year mouse availability explained all variation in territory size ($n = 5$ territories). Myers et al. (1979) and Temeles (1987), however, acknowledged that both factors probably play a key role in territory-size regulation. Ours and the study by Temeles (1987) are the only two that have examined relationships among bird territory size, competitors, and prey in more than one year using partial-correlation analysis. Contrasting with Temeles (1987), we observed the same relationships during both years of our study (Table 2).

We suggest that kite territory size is proximately regulated by competitor abundance and

TABLE 3. Partial-correlation analysis results, for both years combined, using Black-shouldered Kite territory size as dependent variable, and competitor abundance and prey abundance as independent variables.

Independent variables[a]	r	Partial correlation	P for partial correlation	Adjusted r^2	Model P	n
Competitor abundance	−0.762	−0.448	<0.05	0.569	<0.001	25
Microtus density	−0.711	−0.246	0.20 < 0.50			
Microtus density	−0.711	−0.468	<0.02	0.380	<0.001	25
Kite abundance	−0.637	−0.246	0.20 < 0.50			
Competitor abundance	−0.780	−0.446	<0.02	0.613	<0.001	26
Index to numbers of *Microtus*	−0.746	−0.305	0.10 < 0.20			

[a] For each run, only first variable entered into model. Partial correlation for first variable comes from forcing second variable to enter model first.

ultimately regulated by prey abundance, because raptor abundance appeared to be regulated by vole abundance (Fig. 1). Myers et al. (1979) reached the same conclusion about Sanderling territory size. On the beaches inhabited by Sanderlings, food abundance changed rapidly. Myers et al. (1979) suggested that Sanderlings were most influenced by the factor that was least variable (i.e. intruder numbers). Temeles (1987) correctly stated that the strength of a correlation depends partly on the magnitude of variation in the variables examined and that his results could be explained statistically by greater variation in food abundance than intruder variables. Our system is similar in many ways to that studied by Temeles, but we measured both prey and competitor abundance differently. Although we did not examine numbers and types of interactions between territory owners and competitors, we assumed that competitor abundance was positively related to number of interactions between owners and competitors. McFarland (1986) reported a significant positive correlation between numbers of competitors and intrusion rates on his study area. It is unclear when examined over the duration of our study whether vole or competitor abundance is more variable because the two are so closely related (Fig. 1). It is possible that our measure of competitor abundance was more accurate than our measure of prey abundance within territories, which could account for competitor abundance being a better predictor of kite territory size. However, it is unlikely that we would have found such small variation (SE) in our estimate of vole abundance within kite territories if the estimates were not accurate.

We suggest that kites defend as large an area as is energetically feasible at any one time, but that increased competitor abundance reduces the defendable area. Several lines of evidence, some circumstantial, support this contention. Kites can and do adjust territory boundaries with respect to local conditions. Raptors in the Arcata-Eureka area undergo regular annual fluctuations in abundance (Table 1, Fig. 1B), numbers generally increasing in September through October, then remaining relatively constant until March or April, when they decrease dramatically. These fluctuations were closely tied to annual fluctuations of *M. californicus* ($r = 0.90$, $P < 0.001$, $n = 19$, Fig. 1). The largest number of voles estimated to be in a kite territory was 3,340 during mid-August 1990 (territory size was 15.6 ha), which was a time when vole abundance was relatively high, and when many of the winter resident raptors had not yet arrived on the study area. Also, on one occasion we were able to document the precise day that a territory was abandoned by its owner; on that same day the entire territory was incorporated into the territory of a neighboring kite. Village (1982) reported similar results with naturally caused territory abandonment of European Kestrels (*Falco tinnunculus*). Village (1990) experimentally removed European Kestrels from their territories and found that in four of seven instances neighboring birds used vacated territories, but that none of the vacated territories were permanently occupied by "new" birds. However, kestrel territories on Village's study area were much larger (most were greater than 2 km^2; Village 1990) than those of kites on our study area. Thus, dramatic expansions of neighbors into vacated territories might be less likely than on our study area where the largest of 26 territories was 0.22 km^2.

When all raptors were treated as competitors, competitor abundance but not prey abundance influenced territory size of kites. Conversely, when only kites were considered as competitors, prey abundance but not competitor abundance influenced territory size. We believe it is biologically more meaningful to treat all raptors as competitors, rather than conspecifics only. However, defense costs may depend on competitor identity (Temeles 1989, 1990a, b). Kites were commonly observed attacking Northern Harriers, Red-tailed Hawks, Rough-legged Hawks, Red-shouldered Hawks, and other kites. Also, each of the above species, plus American Kestrels and Short-eared Owls were observed to catch and eat *M. californicus* regularly. *Microtus californicus* was by far the most common item in the diet of kites (99%), Red-tailed Hawks (96%), Common Barn-Owls (84%), Short-eared Owls (70%), and Northern Harriers (50%), based on an assessment using regurgitated pellets collected throughout the Arcata/Eureka grasslands (unpubl. data).

During 19 months of small-mammal trapping only four species of small mammals were captured: *M. californicus*, *Reithrodontomys megalotis* (western harvest mice), *Mus musculus* (house mice), and *Sorex vagrans* (vagrant shrews). *Microtus californicus* consistently was the most abundant small mammal and constituted even more of the small-mammal biomass (94%). This along with our findings that the index of *M. californicus* abundance explained 81% of the variation in total raptor abundance strongly suggests that they were the major food source for almost all of the raptors on the study area. Also, kleptoparasitism by hawks on kites was regularly observed. Thus, we considered all species that were using the same food sources to be competitors, as opposed to only conspecifics.

One of our most striking findings was the temporal stability of the estimate of vole abundance within territories, suggesting that kites need about 1,500 voles within their territories. Kites should abandon territories that have much fewer than this number of voles. Apparently, prey abundance and prey availability were correlated in this instance. *Microtus* presumably need a minimum level of cover in order for large populations to survive (Birney et al. 1976). On our study area, voles were virtually absent in grazed areas with vegetation less than 10 cm in height (Cooper unpubl. data). Thus, within areas of dense and tall vegetation, kites needed about 1,500 voles (abundance) so that some were available to foraging kites. Dunk (1992) reported larger vole populations in areas with shorter vegetation (all areas were ungrazed), areas that probably simultaneously maximized their abundance and availability to raptors.

Hunting style and perch availability are also likely to influence raptor territory size. Because kites in California primarily hunt by hovering, we believe their relatively small territory size on our study area was a function of both prey abundance and the fact that they can hunt 100% of their territories. Mendelsohn (1981) reported much larger territory sizes for Black-shouldered Kites (though prey abundances were not reported) in South Africa, where the birds hunt primarily from perches.

Previous researchers of Black-shouldered Kites have reported them to be both territorial and nonterritorial (see review in Henry 1983). We only observed territorial birds, and as a result we are unable to address the role of nonterritorial kites on our study area. Mendelsohn (1981) suggested that kite territoriality would break down at some upper threshold of prey density, but found that South African kites abandoned territories most often when prey populations were low. Possibly, prey populations on our study area never reached this lower threshold. Instead, our findings suggest that territories simply become smaller as a result of increasing competitor abundance (the proximate factor regulating territory size), which is strongly correlated with food abundance (the ultimate factor regulating kite territory size).

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