Impacts of El Niño–Southern Oscillation Events on the Distribution of Wintering Raptors

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ABSTRACT We report the effects of El Niño–Southern Oscillation (ENSO) events on the distribution and abundance of 3 raptor species at continental, regional, and landscape scales. We correlated values from the southern oscillation index (SOI), an index of ENSO phase and strength, with Christmas Bird Count data over a 30-year period. We investigated the relationship between the SOI and winter raptor distributions at 3 spatial scales: continental (central United States), regional (TX, USA), and landscape (3 roadside transects within TX). At the continental scale, ENSO events resulted in regional shifts for American kestrel (*Falco sparverius*), northern harrier (*Circus cyaneus*), and red-tailed hawk (*Buteo jamaicensis*) winter abundances. As expected, these shifts were northward during El Niño (warm) winters, and southward for red-tailed hawks and northern harriers during La Niña (cold) winters. Within Texas, northern harrier distributions shifted towards arid west Texas during wet El Niño winters but were restricted to mesic coastal Texas during dry La Niña winters. Red-tailed hawk abundance increased in eastern Texas during La Niña winters responding to cooler than normal temperatures throughout the northern Midwest. Data from local roadside transects over a 3-year period encompassing 2 El Niño winters and one La Niña winter supported the abundance patterns revealed by continental and regional data, and added evidence that fluctuations in winter abundances result from demographic pulses as well as spatial shifts for wintering populations. This study underscores the need for long-term monitoring at both local and regional spatial scales in order to detect changes in continental populations. Short-term or local studies would have erroneously assumed local population declines or increases associated with ENSO events, rather than facultative movements or demographic pulses supported by this study. (JOURNAL OF WILDLIFE MANAGEMENT 72(1):231–239; 2008)

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The changes in temperatures and precipitation predicted to occur over the next 100 years will have profound impacts on both plant and animal distributions (Iverson and Prasad 1998, Hansen et al. 2001, Price and Root 2001). Furthermore, naturally occurring climate cycles impact the phenology and demography of both individual wildlife species and trophic relationships among species (Sillett et al. 2000, Jaksic 2001, Møller 2002, Morrison and Bolger 2002). El Niño–Southern Oscillation (ENSO) events affect both precipitation and temperature, and ENSO-related variation in weather results in immediate impacts upon wildlife species. Furthermore, natural climate cycles and anthropogenic-influenced climate change may interact, increasing the frequency and severity of El Niño events as the global climate warms (Timmerman et al. 1999). Some variations in the abundance and productivity of wildlife populations currently attributed to error or climate change may result from naturally occurring climate cycles (Sillett et al. 2000, Morrison and Bolger 2002, Anders and Post 2006).

Within the central United States, El Niño events result in warmer winters from the southern Canadian border south to Oklahoma and Arkansas (Halpert and Ropelewski 1992, Ropelewski and Halpert 1996). La Niña weather patterns are generally opposite to those displayed during El Niño events, especially in the northern and southern extremes of the central United States (Halpert and Ropelewski 1992, Ropelewski and Halpert 1996). Changing temperatures associated with ENSO events may affect avian winter distributions by shifting either 1) the thermocline representing the physiological tolerance of the species (Root 1988*a*) or 2) increasing the abundance or the availability of food (Lima et al. 1999). Whereas temperature may directly restrict species distributions, ENSO events affect winter patterns of precipitation more predictably than temperature. The increase in winter precipitation across most of the central United States during El Niño winters may result in favorable breeding conditions the following spring or improved prey availability the following winter, ultimately increasing the abundance of wintering raptors the year following an El Niño event (Lima et al. 1999, 2001).

Although the immediate effects of ENSO events are most noticeable during winter months, they influence weather patterns throughout the year. Nott et al. (2002) concluded that changes to regional weather patterns increased southerly winds, facilitating spring migration for neotropical migrant songbirds returning to the Pacific Northwest during El Niño years. Similar changes to weather patterns in fall and winter may provide a mechanistic framework explaining distribution shifts in both breeding and wintering short-distance migrants. Raptors rely on fall cold fronts to facilitate migration along ridge tops and coastal areas (Kerlinger 1989). El Niño–Southern Oscillation induced disruptions to the jet stream may affect the number and intensity of fall cold fronts, changing both the chronology and passage rate of migrating raptors at regional or

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continental scales. Mild fall and winter weather may result in increases to either winter rodent populations or rodent availability to nonbreeding raptors, allowing individual raptors to remain closer to northern breeding areas (Craighead and Craighead 1956), as well as increase the survival of juvenile raptors resulting in an increase to the regional population through local recruitment.

To investigate the impacts of ENSO events on raptors wintering in the central United States, we selected 3 ubiquitous species: American kestrel (*Falco sparverius*), northern harrier (*Circus cyaneus*), and red-tailed hawk (*Buteo jamaicensis*). All 3 species are partial migrants, where northern populations spend winters in more temperate southern climates, whereas southern populations are resident throughout the year. We investigated the relationship between an objective measure of ENSO severity, the Southern Oscillation Index (SOI), and winter raptor distributions at 3 spatial scales: continental (central United States), regional (TX), and landscape (3 roadside transects within TX).

We hypothesized ENSO events affect winter abundance for all 3 species at 3 different scales. 1) At the continental scale (within the central United States) we predicted that temperature would impact species' distributions, with bird populations remaining further north (especially in the Northern Plains states and Montana) during El Niño (warm) years and that migrants should move further south, into Louisiana, New Mexico, and Texas, during La Niña (cool) years. If these changes are dictated by a species' lower critical temperature, we predict correlation coefficients of greater magnitude for American kestrels compared to larger raptors, as larger body size facilitates heat retention in cold temperatures (Root 1988*a*). However, if prey availability affects species' distributions, then the magnitude of correlation coefficients should be independent of body size. 2) At the regional scale we predicted raptor abundance should mirror precipitation patterns across the state of Texas. Specifically, wintering raptors should concentrate in the xeric western part of the state during El Niño years (warm and wet) and raptor numbers should increase in the mesic coastal areas during La Niña (cool and dry) years in response to fluctuating rodent numbers. 3) At the landscape scale, we predicted patterns of raptor abundance estimated from roadside transects in southeastern Texas would mirror ENSO-driven fluctuations observed at regional and continental scales. Finally, to investigate whether potential changes to species density were due to latitudinal shifts in winter populations or reproductive pulses, we investigated correlations between Breeding Bird Survey (BBS) data with both the Christmas Bird Count (CBC) data and the SOI values.

STUDY AREA

Count Sites, Climate Regions, and Roadside Transects

We selected CBC circles based on their location within the BBS's central region (Sauer et al. 2006). We limited our choices to circles with either 1) continuous data for $\geq$20 years (1980–1999) or 2) $\geq$30 years of data with $\leq$5 years of missing data and $\leq$2 years missing in any 5-year span. We divided the central United States into 5 regions based on deviations from temperature and precipitation patterns during El Niño events (Livezey et al. 1997; Fig. 1). We standardized count effort to approximately one circle per 4,000–4,300 km^2 of land area for all regions.

Our 5 continental climate regions were Montana, Northern Plains, Rocky Mountains, Southern Plains, and South (Fig. 1). The Montana region, characterized by warm and dry weather during El Niño events, included 4 count circles in Montana. The Northern Plains region, included 12 circles in North Dakota, South Dakota, and Minnesota, displayed warmer than normal temperatures during El Niño events. The Rocky Mountain region was composed of 11 count circles from Colorado, Wyoming, and the westernmost circle in Nebraska; winter weather conditions did not deviate from normal during El Niño events. The Southern Plains region included 27 count circles from Kansas, Nebraska, Oklahoma, Missouri, Arkansas, and Iowa, and was warm and wet during El Niño events. The South region was composed of 27 count circles from Texas, New Mexico, and Louisiana, and displayed wetter than normal conditions during El Niño events.

For the state level analysis we divided Texas into eastern and western areas based on the 10 climate regions of Texas (Bridges et al. 2001; Fig. 2). Christmas Bird Count circles in eastern Texas experienced mesic conditions due to the influence of the Gulf of Mexico. Representative vegetation communities were dominated by tall-grass prairies or mixed oak–pine forests. In contrast, CBC circles from xeric western Texas were in landscapes dominated by short-grass prairie or desert-shrub lands.

At the landscape scale, our study included 3 roadside transects in southeastern Texas (Fig. 2) surveyed from 1998 to 2000, which encompassed one El Niño year and a 2-year La Niña event. We surveyed transects early to mid morning, following the methodology of Fuller and Mosher (1981). Whenever possible we recorded the age and sex of raptors. The 3 transects were situated along an east–west gradient characterized by decreasing moisture and agricultural intensity and a corresponding increase of woody vegetation abundance. Transect 1 extended 80 km on State Highway 71 from Altair, Texas, south to the junction of State Highway 35 in Colorado, Wharton, and Matagorda counties. Transect 2 was 46 km in length along Texas farm road 774 from Austwell, Texas to Refugio, Texas in Refugio County. Transect 3 was 63 km long and followed farm road 2295 from Highway 281 west to Benavides, Texas, and then State Highway 339 to Highway 16 near Freer, Texas, in Jim Wells and Duval counties.

Breeding Bird Survey

The BBS is an ongoing landbird census collecting data from >3,000 individual routes in the United States and Canada (Sauer et al. 2003). Each route is approximately 40 km in length, with 50 stops spaced 0.8 km apart. Data are reported as the number of birds seen or heard per route. Because

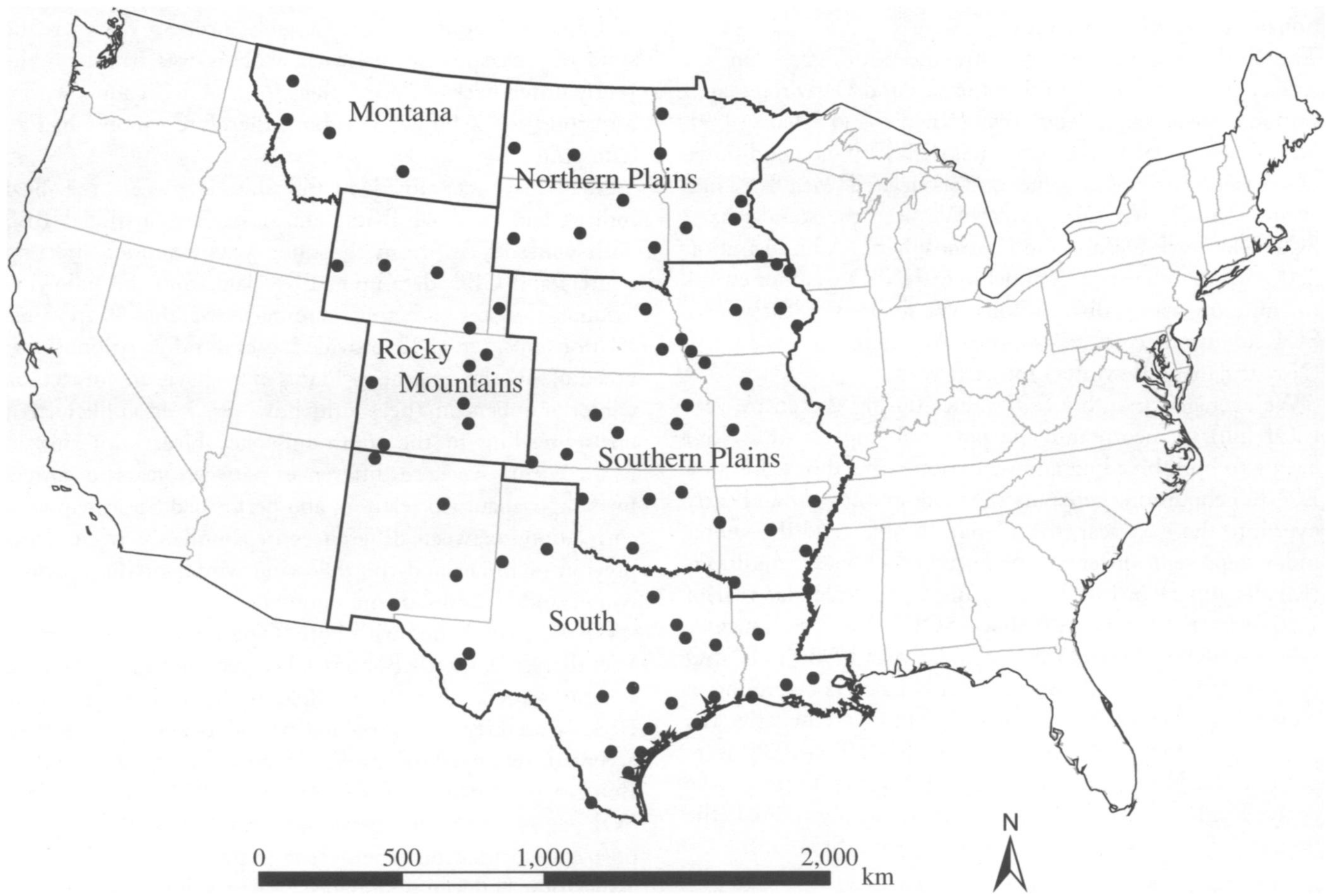

Figure 1. Climate regions and Christmas Bird Count circles within the central United States used to examine the effects of El Niño–Southern Oscillation events on wintering raptors, 1970–1999. Climate regions were defined by departures from normal temperature and precipitation conditions during El Niño events.

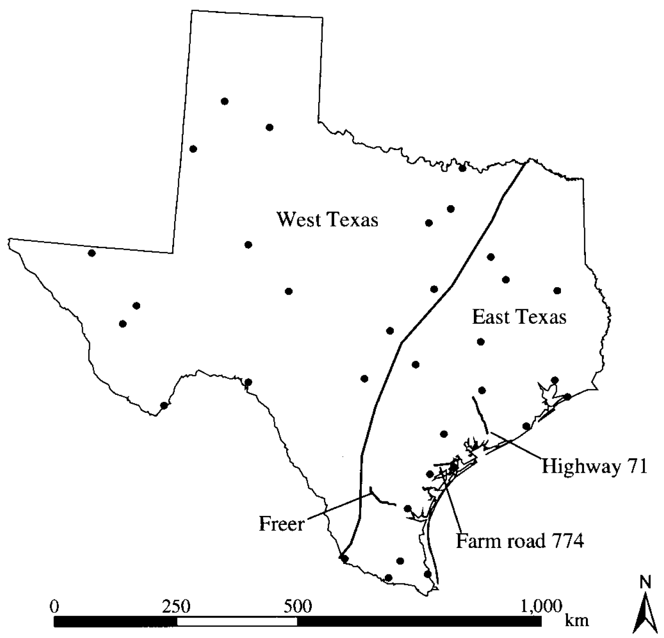

Figure 2. Texas, USA, divided into eastern and western sections based on ecoregion affiliation. West Texas counties represent dry grasslands and desert shrubland ecotypes whereas east Texas counties represent coastal grassland, forest, and shrubland ecosystems. Points represent Christmas Bird Count locations and thick lines represent location of roadside transects used in the regional and landscape analyses.

breeding raptors have large territories, BBS routes were not the most effective means to estimate population densities. However, BBS routes do provide an unbiased index of summer abundance to test causal relationships between breeding and wintering populations, such as whether winter population increases are the result of increased breeding effort or if increased winter survival results in spikes to breeding populations. We downloaded the average number of birds seen per route adjusted for the area of the entire state, from 1970 to 2000 for each of the 15 states (Sauer et al. 2006). We calculated average species abundance for each of the 5 continental climate regions.

METHODS

Christmas Bird Count Data

The CBC collects information on wintering bird abundance throughout the United States, southern Canada, and northern Mexico. Annual counts occurred within a 24.1-km-diameter circle on 1 day between 11 December and 8 January. Our study species were traditionally abundant and easily identified by CBC participants due to their relatively large size or use of exposed perches (Fuller and Mosher 1981). We downloaded 30 years (1970–1999) of CBC data from National Audubon Society website (National Audubon Society 2002).

Southern Oscillation Index

The SOI measures the monthly mean difference in sea surface pressure from Tahiti in the east and Darwin research station, Australia, in the west (Kiladis and Diaz 1989). Negative SOI values are associated with El Niño conditions, whereas positive SOI values are associated with La Niña events (Kiladis and Diaz 1989). We used the standardized SOI (National Oceanic and Atmospheric Administration 2000) to examine the relationship of ENSO weather events to wintering raptor distributions. We focused on the winter SOI conditions close to National Audubon Society's CBC (Nov to Jan, SOI-winter) for each year.

We averaged monthly SOI values during the entire year (SOI-full) to incorporate the potential impacts of ENSO events to both breeding and wintering populations. Because El Niño conditions generally start late in one year and carry over into the next year, the 12-month index and the winter index represent different measures of climate conditions (Kiladis and Diaz 1989). For example, the calendar year of 1997 was an El Niño year, both SOI-full and SOI-winter values were negative. During calendar year 1998 the ENSO cycle switched from El Niño to a La Niña cycle beginning in November. The 1998 values for SOI-full were negative (El Niño), but the SOI-winter values for 1998–1989 were positive (La Niña). Finally, because ENSO cycles may have delayed effects on regional weather, we examined the impacts of SOI events from previous years (SOI-lag).

Statistical Analyses

We standardized CBC count data to number of individuals counted per 1,000 km traveled (birds/1,000 km) for each species. The 3 raptor species we studied are traditionally surveyed through road transects because they are conspicuous either perched or foraging (Fuller and Mosher 1981). One or two observers can effectively monitor these species, therefore we believe the traditional transformation, birds per party-hour, was not as important as number of birds detected per distance traveled. As the abundance of both red-tailed hawks and American kestrels displayed significant increases over time, we detrended data by examining differences between years ($\text{year}_{(I+1)} - \text{year}_{(I)}$) for abundance values (both CBC and BBS) and SOI measurements (Sokal and Rohlf 1995).

We ranked SOI and species abundance data to investigate ENSO-influenced trends using Spearman's rank correlations for each species per region grouping for winter, full-year, and full-year lagged values of the SOI. We calculated Spearman's rank correlations for each SOI measured against differences in raptor abundance from the entire state of Texas, coastal counts, and interior counts in relationship to different SOI measurements. We ran all correlations using Minitab 12.0 (MINITAB, State College, PA)

Roadside transect data were recorded between January 1998 and March 2000 for an unrelated study, but these independent data sets allowed us to look for congruence with both predictions and results from the continental and regional scales. We had large data sets, 2,316 counts from 81 CBC sites over 30 years for the entire central United States and 531 counts using 31 CBC sites over 30 years for the state of Texas. However, each analysis was based on the yearly differences of mean values for all CBC counts within a region (no. of birds/1,000 km), therefore we only had 29 data points for each analysis.

Finally, we examined relationships between the SOI indices and regional BBS data, as well as regional BBS with winter CBC from the same year (summer affecting winter) and CBC data upon BBS data from the following summer (winter affecting summer). Of the 50 possible relationships, only 32 provided useful information (birds breeding in the Southern Plains may have an impact on winter numbers in the south; however, it is unlikely that birds breeding in the south influence birds wintering in MT). Again, we used differences between years to correct for temporal autocorrelation, and performed Spearman rank correlations between differences in abundance from either previous summer and the following winter or the previous winter and the subsequent summer.

We were concerned with both Type I and Type II errors. We, therefore, used a Bonferroni correction to avoid a Type I error associated with multiple tests of the same data. Because each region represented an independent data set, we accepted relationships as significant at $\alpha = 0.1$, with a Bonferroni adjustment for 3 tests ($P = 0.033$) for each of the SOI-values. For all correlations involving the SOI, a positive correlation coefficient represented a negative association between abundance (lower abundance) and the El Niño phase of the southern oscillation and a positive relationship with the La Niña phase of the SOI. We examined relationships among summer and winter regions at an $\alpha = 0.1$ Bonferroni adjustment for 5 tests ($P = 0.02$), because we tested each region against all possible regions.

RESULTS

Northern Harriers

Christmas Bird Count abundance of northern harriers from the entire central United States did not change over the 30-year study period. Harrier abundance in the entire central United States and within the Rocky Mountain region displayed negative correlations with the SOI-lag values (Table 1), and therefore winter abundances often doubled the winter following El Niño years both across the central United States and within the Rocky Mountain region. In the Southern Plains region, harrier counts displayed negative correlations with full-year SOI values (Table 1), often doubling in abundance during El Niño winters but falling below pre-El Niño levels during La Niña phases.

In Texas, winter harrier counts across the state did not change in response to changes in SOI; however, harrier counts within the eastern and western parts of the state were correlated with SOI-winter values (Table 1). Specifically, harriers in the western part of Texas decreased by 1.5 individuals per 1,000 km for each unit of SOI, whereas harrier abundance in the eastern part of the state increased by an average of 3 individuals per 1,000 km for each SOI unit. Harrier abundance was low along all 3 roadside

Table 1. Spearman rank correlation coefficients between Southern Oscillation Index (SOI) values and Christmas Bird Count abundance for northern harriers, red-tailed hawks, and American kestrels from 5 different climate regions within the central United States and regional analysis for the Texas, and the eastern and western parts of the state from 1970 to 1999.[a]

	Continental						TX		
	MT	Northern Plains	Rocky Mountains	Southern Plains	South	Central USA	All	Eastern	Western
SOI-winter[b]									
Northern harrier	−0.069	−0.080	0.364	−0.268	0.354	0.226	0.177	0.444*	−0.434*
Red-tailed hawk	−0.159	0.111	0.079	−0.437*	0.489**	−0.001	0.465**	0.589**	−0.200
American kestrel	0.079	−0.541**	−0.017	−0.471**	0.042	−0.249	0.026	−0.065	0.120
SOI-full[c]									
Northern harrier	0.123	0.130	0.030	−0.453**	0.073	−0.166	0.032	0.144	−0.119
Red-tailed hawk	−0.527**	−0.171	0.025	−0.143	0.069	−0.230	0.171	0.237	−0.037
American kestrel	0.068	−0.412*	0.060	−0.256	−0.224	−0.341	−0.140	−0.198	0.091
SOI-lag[d]									
Northern harrier	−0.014	−0.174	−0.519**	0.053	−0.371	−0.436*	−0.204	−0.402*	0.334
Red-tailed hawk	0.116	−0.001	0.168	0.245	−0.620**	−0.132	−0.400	−0.537**	0.068
American kestrel	−0.042	0.106	−0.215	0.111	−0.310	−0.237	−0.124	−0.187	0.064

[a] Climate regions were Montana (MT), Northern Plains (MN, ND, and SD), Rocky Mountains (CO, WY, and western NE), Southern Plains (AR, IA, KS, MO, eastern NE, and OK), and South (LA, NM, and TX). Negative associations indicate a positive relationship between species abundance and El Niño events, whereas positive coefficients are associated with La Niña events.
[b] SOI-winter refers to SOI values averaged over Nov, Dec, and Jan.
[c] SOI-full refers to SOI values averaged over all 12 months within a calendar yr.
[d] SOI-lag refers to SOI values averaged from the previous yr.
* $P \leq 0.1$ Bonferroni corrected to $P \leq 0.033$.
** $P < 0.05$ Bonferroni corrected to $P \leq 0.016$.

transects, often resulting in zero counts, preventing analyses at the landscape scale.

Northern harrier abundance decreased 2.6% per year for all BBS routes within the central region from 1966 to 2005 (Sauer et al. 2006). Within the Southern Plains and Rocky Mountain regions harrier abundance declined from 1970 to 1999, whereas no significant trends were present in the Montana and Northern Plains regions. Breeding harrier abundance increased in the Northern Plains following El Niño winters ($r_s = -0.435$ $P = 0.018$ SOI-lag), but no other ENSO-related observations were significant for breeding birds. None of the correlations between summer and winter regions resulted in significant relationships (Table 2).

Red-Tailed Hawks

Average winter red-tailed hawk abundance increased 2.8% per year ($P < 0.01$) over the 30-year sampling period across the entire central region. Winter red-tailed hawk counts increased during El Niño events (negatively correlated with full-year SOI values) in the Montana region. Hawk abundance within Southern Plains CBCs also fluctuated with both El Niño and La Niña events respectively (Table 1), whereas red-tailed hawk abundance at count sites in the South region decreased during El Niño events and increased during La Niña events and years following El Niño events (Table 1).

Red-tailed hawk abundance from CBC sites both across Texas and in the eastern section of the state were positively associated with La Niña events (east TX populations increased an average of 5 individuals per 1,000 km for every 1 unit of SOI increase). Counts in eastern Texas also displayed a strong negative association with SOI-lag values, with increasing hawk abundance the winter following El Niño events. Roadside counts of wintering red-tailed hawks in southeastern Texas increased 92–294% in response to the switch from El Nino (1998) to La Nina conditions (1999–2000; Fig. 3), supporting both the continental and regional patterns. The age distribution of red-tailed hawks shifted from adults to juveniles, more than doubling the proportion of juveniles detected along all transects from winter 1998 to winter 1999 (Table 3). In winter 2000, the age distribution shifted back to the adult bias observed during winter 1998.

Red-tailed hawk abundance on BBS routes increased an average of 4.8% per year within the central BBS region from 1966 to 2005 (Sauer et al. 2006). Red-tailed hawk abundance in the Southern Plains exhibited were correlated with average SOI ($r_s = -0.429$, $P = 0.020$), whereas populations in the Northern Plains displayed a relationship with SOI values from the previous year ($r_s = -0.421$, $P = 0.023$). Summer abundance in the Montana region displayed a positive correlation with winter abundance in the Rocky Mountain region, whereas winter abundance in the Montana region displayed a positive correlation with summer abundance in the Northern Plains region (Table 2).

American Kestrels

American kestrel winter abundance increased approximately 0.5% per year over the 30-year sampling period within the central United States ($P < 0.01$). American kestrel winter abundance correlated with full-year SOI values in the Northern Plains region, and winter SOI-values from both the Northern and Southern Plains. All associations between winter counts and SOI-values were negative, therefore winter populations in both the Northern and Southern Plains increased during El Niño events and decreased during La Niña events (Table 1, Fig. 4). There were no correlations

Table 2. Spear rank correlation coefficients relating Breeding Bird Survey (summer) abundance (rows) to the Christmas Bird Counts (winter) abundance the following winter (columns) or relating winter abundance (columns) to abundance from the following summer (rows) for northern harrier, red-tailed hawk, and American kestrels occurring within 5 climate regions from the central United States from 1970 to 1999.[a]

	Summer predicts winter					Winter predicts next summer				
Species and region	**MT**	**Northern Plains**	**Rocky Mountains**	**Southern Plains**	**South**	**MT**	**Northern Plains**	**Rocky Mountains**	**Southern Plains**	**South**
Northern harrier										
MT	−0.006	−0.327			NA	0.206	0.017			NA
Northern Plains	0.219	0.106	0.420		NA	−0.076	0.192	−0.229		NA
Rocky Mountains	0.159	−0.059	−0.109	−0.078	NA	0.000	−0.150	0.231	0.307	NA
Southern Plains	0.085	0.047	0.308	−0.019	NA	0.081	0.158	−0.199	0.334	NA
South	−0.277	−0.279	−0.059	0.041	NA	−0.303	−0.329	−0.072	0.021	NA
Red-tailed hawk										
MT	0.051	−0.229				−0.071	0.478*			
Northern Plains	−0.222	−0.006	−0.193			0.107	0.339	0.042		
Rocky Mountains	0.551*	−0.118	0.141	−0.218		−0.328	0.102	0.099	0.392	
Southern Plains	0.149	−0.059	−0.000	0.289	0.126	−0.314	0.245	−0.109	0.148	0.179
South	−0.149	0.371	−0.359	−0.003	0.283	0.164	−0.223	0.254	−0.252	−0.402
American kestrel										
MT	−0.088	0.066				0.185	−0.096			
Northern Plains	−0.007	−0.072	0.366			−0.066	0.162	−0.421		
Rocky Mountains	0.008	0.036	0.240	0.057		0.105	0.083	−0.089	0.042	
Southern Plains	−0.154	0.117	0.040	0.009	0.223	0.261	−0.019	−0.178	0.253	−0.166
South	−0.014	0.179	−0.322	0.098	−0.123	0.249	0.137	0.428	−0.017	0.166

[a] Climate regions were Montana (MT), Northern Plains (MN, ND, and SD), Rocky Mountains (CO, WY, and western NE), Southern Plains (AR, IA, KS, MO, eastern NE, and OK), and South (LA, NM, and TX). NA = data not available.
* $P \leq 0.05$ Bonferroni corrected to $P \leq 0.01$.

between SOI and kestrel densities across Texas, or between western and eastern parts of the state. For all 3 roadside transects, kestrel abundance was 20–80% greater during the 2 La Niña winters compared to the El Niño winter (Fig. 5).

American kestrel abundance on BBS routes in the central United States increased 4.8% per year from 1966 to 1979, but kestrel numbers decreased 1.3% per year from 1980 to 2005 (Sauer et al. 2006). Associations between winter kestrel abundance from the Northern Plains and South regions were nearly significant with subsequent summer abundance in the Rocky Mountain region (Northern Plains $P = 0.023$, South region $P = 0.021$; Table 2) from 1970 to 1999.

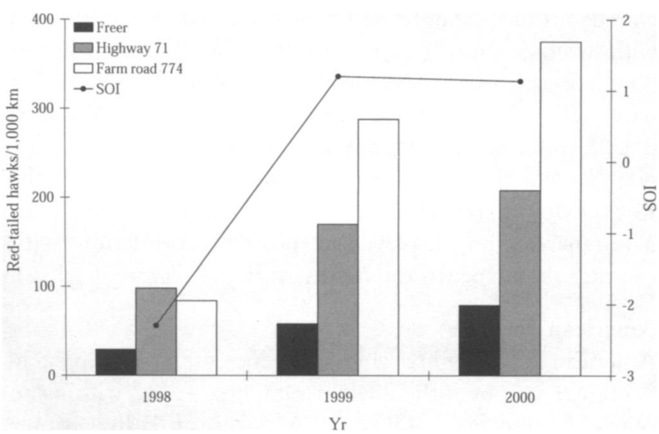

Figure 3. Annual winter abundance for red-tailed hawk along roadside transects (bars) and the line represents winter values for the Southern Oscillation Index (SOI) from 1998 to 2000. All transects were in southeastern Texas, USA. Highway 71 transect was located in Colorado, Matagorda, and Wharton counties; Farm road 774 transect was located in Refugio County; and Freer transect was located in Duvall and Jim Wells counties. We averaged all abundance data from October to March. Year corresponds to January from that winter.

DISCUSSION

Continental Scale

The responses of northern harrier and red-tailed hawk populations to ENSO events were consistent with our first hypothesis of temperature-mediated movements within the central United States. Red-tailed hawks displayed the greatest association within the Montana region during warm years, but winter abundance of all 3 species displayed positive associations with El Niño events within the Southern Plains. American kestrel abundance patterns at the continental scale were consistent with ENSO-related temperature responses in the northern part of the study area, but CBC sites in the South region never displayed increases during the colder La Niña ENSO-phase. For all 3 species, warmer El Niño winters allowed nonbreeding raptors to remain further north by either reducing daily energy expenditure or by increasing prey availability (LeFebvre and Raveling 1967, Jaksic et al. 1997, Jaksic and Lazo 1999).

Breeding Bird Survey data revealed increased red-tailed hawk and northern harrier breeding abundance in the Northern Plains region following El Niño events concordant with the demographic pulse hypothesis. Furthermore, red-tailed hawk population trends in the Southern Plains corresponded to El Niño events during both breeding and winter seasons, whereas red-tailed hawk populations in the South region displayed positive associations with the SOI consistent with La Niña events. Increased breeding

Table 3. Age distribution (%) of adults and juveniles and total numbers (*n*) for red-tailed hawks encountered during surveys of roadside transects in south Texas, USA, conducted October–March, during 3 winters (as defined by Jan) 1998–2000.

	Transect								
	Farm road 774			Highway 71			Freer		
Yr	Ad	Juv	*n*	Ad	Juv	*n*	Ad	Juv	*n*
1997–1998	76	24	21	92	8	48	86	14	7
1998–1999	41	59	139	79	21	117	63	37	27
1999–2000	83	17	111	87	13	110	66	34	41

populations in the Montana region resulted in increased winter populations in the Rocky mountain region. Although not as clear, elevated winter populations in the Montana region were correlated with increased breeding populations the following year in the Northern Plains. Red-tailed hawks were the only species we examined displaying relationships amongst regions during consecutive summer–winter or winter–summer periods, and then only 2 of 38 relationships proved significant. The lack of significant relationships for both the kestrel and harrier may be biologically accurate, but the lack of relationships may also reflect bias inherent in summer survey methods.

Regional Scale

Within Texas only northern harrier winter populations conformed to our hypothesis of interchange between eastern and western Texas related to ENSO-mediated changes in precipitation. Changes in red-tailed hawk abundance were not consistent with population movements within Texas, but they supported the latitudinal shifts at the continental scale. American kestrel CBC abundance did not fluctuate with ENSO conditions within Texas.

Landscape Scale

American kestrel abundance along roadside transects increased 20–80% during La Niña winters compared to the El Niño winter. In all 3 winters peak kestrel abundance occurred during the mid-late January, too early for CBC sites in the south to record the influx of birds during unusually cold winters, explaining the lack of ENSO-related patterns to kestrel abundance data in the South region or within Texas. Alternatively, red-tailed hawk roadside survey data reinforced the CBC trends at both continental and regional scales. In addition, red-tailed hawks along roadside transects displayed a disproportionate increase in the numbers of juvenile-plumaged birds the first year after an El Niño event. The increase in juvenile plumage birds was consistent with both a demographic pulse and differential migration between the ages during La Niña events, but because the number of red-tailed hawks remained elevated during the second La Niña year but the percentage of juveniles decreased, we conclude that our data support the El Niño–associated demographic pulse hypothesis.

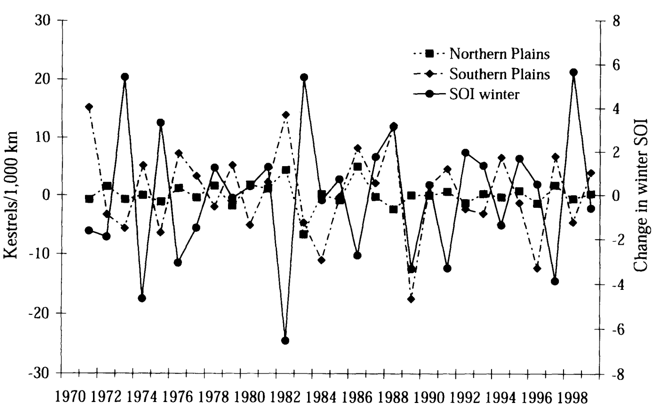

Figure 4. Detrended American kestrel abundance and winter (Nov, Dec, Jan) Southern Oscillation Index (SOI) from 1971 to 1999. Kestrel abundance from the Northern Plains, USA (MN, ND, and SD) and Southern Plains, USA (AR, IA, KS, MO, eastern NE, and OK) are both out of phase with winter-SOI values.

Mild conditions associated with El Niño events allow for several responses by wintering in individuals. Benefits gained by individuals remaining close to breeding areas include earlier initiation of both primary and replacement clutches and, for breeding harriers, polygyny in years of increased food abundance (Hammerstrom et al. 1985). In contrast, La Niña winters appeared to increase red-tailed hawk abundance in the South and Southern Plains regions of our study area due to severe winter temperatures or decreased prey availability in northern areas, likely resulting from snow accumulation or declines in prey populations. We hypothesize that the increase to red-tailed hawk winter abundance in Montana correlated with conditions conducive to summer rodent availability in the Northern Plains, mirroring events documented in Chile (Jaksic and Lazo 1999, Jaksic 2001).

Although changes in kestrel abundance tracked ENSO events at the landscape scale, changes in kestrel numbers at the continental scale may not be apparent for 2 reasons: 1) wintering kestrel abundances are already at their peak in the southern United States (Root 1988*b*) and any additional kestrels may be forced to continue further south, leap-frogging the southern states into Latin American countries thereby bypassing CBC circles during the count period; or 2) winter abundance for kestrels peak in mid-January (Mills 1975, Kim 2001), therefore CBC surveys occur too early to record winter peaks in the southern United States. Breeding season data from the Rocky Mountain region concur with kestrel increases observed during winter in both the Northern and Southern Plains regions, implying kestrels

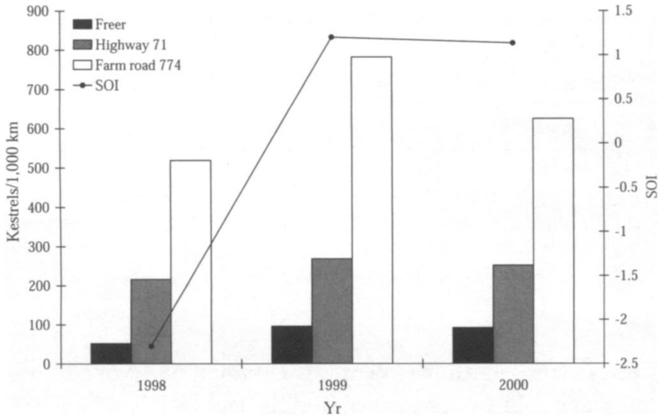

Figure 5. Annual winter abundance for American kestrel along roadside transects (bars) and the line represents winter values for the Southern Oscillation Index (SOI) from 1998 to 2000. All transects were in southeastern Texas, USA. Highway 71 transect was located in Colorado, Matagorda, and Wharton counties; Farm road 774 transect was located in Refugio County; and Freer transect was located in Duvall and Jim Wells counties. We averaged all abundance data from October to March. Year corresponds to January from that winter.

along the front range of the Rocky Mountains move east into the plains states during winter.

Two multiyear studies focusing on wintering raptors support our landscape scale data. Lish and Burge (1995) and Williams et al. (2000) studied red-tailed hawks in Oklahoma and Kansas, respectively, and both studies displayed spikes in wintering red-tailed hawk abundance in the Southern Plains region during El Niño years. Data from Kansas in 1997–1998 (Williams et al. 2000) represented the highest recorded values for wintering red-tailed hawk abundance and also corresponded to the lowest red-tailed hawk abundance recorded in southern Texas (winter 1997–1998; Kim 2001), implying interannual movements of wintering raptors are associated with regional weather conditions.

Conclusions

Impacts of ENSO events were evident at all 3 spatial scales. Observed shifts in continental abundance for red-tailed hawks, American kestrels, and northern harriers may be attributable to either facultative movements of individuals or to changes in mortality and recruitment rates within local populations. Increases in wintering bird densities due to demographic pulses received support from an increase in the proportion of wintering juvenile red-tailed hawks along roadside transects one year after El Niño events. Facultative movements of populations responding to ENSO events received independent support from 2 winter raptor studies in the Southern Plains region of the central United States (Lish and Burge 1995, Williams et al. 2000). Furthermore, the relationship between breeding red-tailed hawks in 2 of the northern regions (Northern Plains and Rocky Mountains) and conditions associated with the SOI imply individuals are moving throughout the central region in response to favorable local conditions.

MANAGEMENT IMPLICATIONS

Our results underscore the need for long-term monitoring and larger scales of study to adequately address winter raptor population changes in the central United States. Short-term or local studies would have erroneously assumed either local declines or increases to winter raptor populations. Population level studies conducted on a local scale should consider regional climate patterns in interpreting their results throughout the central United States because dramatic changes in abundance from one year to next may be more a result of regional distribution patterns than locally influenced processes. Our data suggest population level studies of raptors in the central United States should be of sufficient duration period to include contrasting periods of the ENSO cycle. In addition, population studies of raptors should be conducted at appropriate spatial resolution to adequately incorporate variations on local areas influenced by large scale weather patterns. Data sets, such as the CBC, have broad applicability and have been widely used for evaluating population changes at continental scales, but we found the CBC counts occurred too early to measure peak abundance of wintering raptors in southern areas. Therefore, studies using CBC for evaluating raptor populations in the Central United States should be supported by additional regionally-gathered data sources. The severity of future ENSO events is projected to increase as the global climate warms, increasing the potential for weather-related impacts on wildlife populations at local scales due to severe weather, such as blizzard, extended cold or warm periods, hurricanes, drought, or flooding.

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