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REPRODUCTION, PREY, AND HABITAT OF THE APLOMADO FALCON (*FALCO FEMORALIS*) IN DESERT GRASSLANDS OF CHIHUAHUA, MEXICO

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Abstract.—A breeding population of Aplomado Falcons (*Falco femoralis*) remains in the desert grasslands of Chihuahua, Mexico, despite their extirpation in the nearby southwestern United States. We monitored falcon reproduction at 35 territories during 1996–2002, a period of severe drought in the region. To test the influence of prey abundance and vegetation on falcon reproduction, we surveyed avian prey abundance through plot counts in 1998–2002 and characterized vegetation at each plot. Aplomado Falcon productivity declined from 1.57 fledglings per occupied territory in 1997 to 0.63 in 2002 at the larger of two study areas, a trend consistent with cumulative effects of consecutive years of low rainfall. Reproduction in the smaller area remained low throughout the study. Both productivity and incubation start date were significantly associated with prey bird abundance. Summer rain most likely influenced falcon reproduction by affecting seed abundance and therefore abundance of granivorous prey birds the following winter and spring. Falcons nested in open grasslands with sparse woody vegetation, an adaptation likely related to higher prey vulnerability and fewer predators. However, important prey birds were positively correlated with woody-plant density, which suggests that proximity of shrublands increased nest-site suitability. *Received 17 October 2003, accepted 23 February 2004.*

Resumen.—Una población reproductiva del halcón *Falco femoralis* persiste en los pastizales desérticos de Chihuahua, México, a pesar de haber desaparecido de las áreas aledañas del suroeste de los Estados Unidos. Monitoreamos la reproducción de estos halcones en 35 territorios desde 1996 hasta 2002, durante un período de sequía severa en la región. Para determinar la influencia de la abundancia de presas y de la vegetación sobre la reproducción de *Falco femoralis*, estimamos la abundancia de aves presa en parcelas de conteo desde 1998 hasta 2002 y caracterizamos la vegetación de cada parcela. La productividad de *Falco femoralis* disminuyó de 1.57 volantones por territorio ocupado en 1997 a 0.63 en 2002 en la más grande de las dos áreas de estudio, una tendencia consistente con los efectos acumulativos de varios años consecutivos de baja precipitación. La reproducción en el área más pequeña se mantuvo baja durante todo el estudio. Tanto la productividad como la fecha de inicio de la incubación estuvieron significativamente correlacionadas con la abundancia de aves presa. Las lluvias de verano probablemente influenciaron la reproducción de los halcones al afectar la abundancia de semillas y en consecuencia la abundancia de aves presa granívoras en el siguiente invierno y primavera. Los halcones anidaron en pastizales abiertos con poca vegetación leñosa, una adaptación probablemente relacionada con una mayor vulnerabilidad de las presas y con menos depredadores. Sin embargo, algunas aves importantes como presa se correlacionaron positivamente con la densidad de plantas leñosas, sugiriendo que la proximidad de matorrales incrementa la calidad del sitio de nidificación.

The Northern Aplomado Falcon (*Falco femoralis septentrionalis* Todd) is a medium-sized, savanna-dwelling bird predator whose historical distribution extended from the grasslands of southern and western Texas, southeastern Arizona, and southern New Mexico southward through Mexico to Nicaragua. It had disappeared as a breeding species in the United States by the mid-1900s (Keddy-Hector 2000). Factors that led to its extirpation and those preventing its recovery remain uncertain, but the most strongly

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suspected are habitat deterioration associated with overgrazing during 1870–1890 (Hastings and Turner 1965) and agricultural use of DDT after 1946 (Kiff et al. 1980). Other contributing factors may include lead ingestion, electrocution, collisions with fences and power lines, drowning in livestock watering tanks, and the extirpation of the prairie dog (*Cynomys ludovicianus*) (Keddy-Hector 2000, Truett 2002).

In the early 1990s, Montoya (1995) discovered a previously unknown population of Aplomado falcons in the Mexican state of Chihuahua (Montoya et al. 1997). Because no other population of Aplomado Falcons has been reported north of the eastern coastal plain of Mexico, some 1,100 km distant, their presence in Chihuahua is of considerable conservation interest and provides an opportunity to understand the ecology of the falcons in desert grasslands similar to those in the United States (Dick-Peddie 1993, Powell 2000), where restoration efforts have recently begun.

Because it is near the extreme of the Aplomado Falcon's historical range, one might expect marginal breeding conditions for the population in Chihuahua. Truett (2002) compared published data on breeding-season surveys of birds of the sizes preyed on by Aplomado Falcons (Hector 1985) and found that densities and biomass differed by an order of magnitude between the coastal plain of eastern Mexico and southern Texas and the desert rangelands of Chihuahua and southwestern New Mexico. Some of that disparity is related to differences in precipitation, and some almost certainly to human-related changes in habitat structure. Severe drought in the Chihuahuan Desert region since about 1992 (Melgoza et al. 1998, C. Miller unpubl. data) and persisting at least through 2002 can be expected to have reduced prey availability in Chihuahua overall. Here, we examine the trend of falcon reproduction, its relationship to prey bird numbers in two study areas over a five-year period, and influence of vegetation structure on prey distribution.

METHODS

STUDY AREA

Our work was conducted in the north-central part of the state of Chihuahua, within two study areas: Sueco (~570 km²; extreme coordinates: 29°36′N, 105°57′W, and 30°17′N, 106°28′W) in the municipalities of Ahumada and Chihuahua, and Tinaja Verde (~280 km²; extreme coordinates: 29°41′N, 105°13′W, and 29°52′N, 105°25′W) in the municipality of Coyame. Topography in both areas consists of extensive plains and low hills among mountain ranges. Altitude at nest sites varies from 1,383 to 1,893 m, and slope from 0.0 to 6.7%. Climates are temperate semiarid and temperate arid, with mean annual temperatures of 18–22°C. Average annual rainfall differs between the study areas: 200–300 mm at Sueco and 300–400 mm at Tinaja Verde (CONABIO 1997a–f). Precipitation is largely restricted to thunderstorms occurring during July–September, the distribution of which is patchy and irregular in both study areas. Figure 1 provides data on the drought prevalent during our study.

The Tinaja Verde study area comprises six large, private cattle ranches, where long-term range management has favored higher-quality grasslands than those in most areas of the Sueco study area (Fig. 2), where land use and ownership is more diverse and includes some cultivated fields. Sueco nest sites are more heavily grazed than those at Tinaja Verde; mean percentage of bare ground within 500 m of nests was 63.5% (range = 44.7–75.6, SD = 10.4) at Sueco and 38.8% (range = 26.0–60.8, SD = 9.8) at Tinaja Verde. Open grasslands and open halophyte grasslands predominate in both study areas (Blanco et al. 1978), interspersed with Chihuahuan desert scrublands. Open grasslands are dominated by *Bouteloua gracilis*, *B. hirsuta*, and *B. eriopoda*, with *B. curtipendula*, *Aristida* spp., *Hilaria mutica*, and *Enneapogon desvauxii* as subdominant species. It is common to find those areas noticeably invaded by woody species such as *Acacia constricta*, *Ephedra trifurca*, *Flourensia cernua*, and *Larrea tridentata*. Open halophyte grassland typically occurs in swales and is characterized by *H. mutica* and *Sporobolus airoides*; other grasses, such as *B. gracilis* and *Panicum obtusum*, are also present. The most common woody plants are *Prosopis glandulosa*, *Koeberlinia spinosa*, *F. cernua*, *A. constricta*, and *Condalia ericoides*.

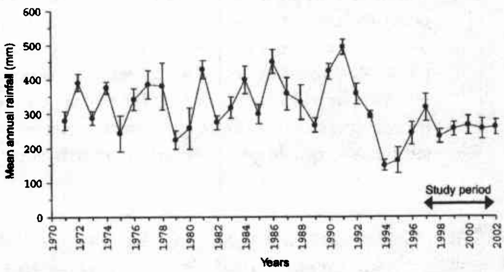

FIG. 1. Mean annual rainfall recorded at six meteorological stations in the arid part of Chihuahua State (Ascensión, Janos, Nuevo Casas Grandes, Las Lajas, Luis L. León, and Camargo) from 1971 to 2002. Vertical bars are standard errors. Data by courtesy of Comisión Nacional del Agua, Mexico.

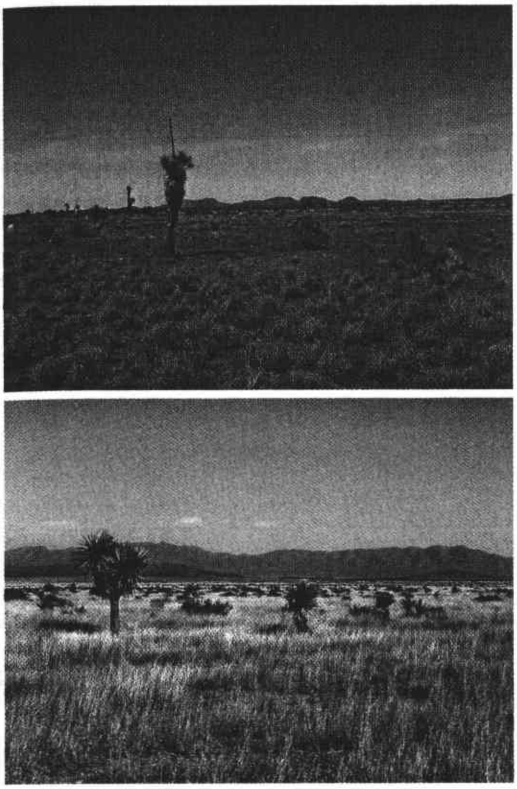

FIG. 2. An example of differences in grassland condition between Sueco nest sites (upper photo) and Tinaja Verde nest sites (lower photo). On average, Tinaja Verde receives more rainfall and less grazing pressure than Sueco.

FALCON SURVEYS

We defined occupied territory as that containing one or more nests of mated pairs, an active territory as one where eggs were laid, and population productivity as average number of fledglings per occupied territory (Postupalsky 1974). Our approach in monitoring falcon reproduction was to find and monitor as many occupied and active territories as possible within the two study areas delineated by Montoya (1995); no systematic sampling or census method was used. By 2002, we had monitored 24 territories at Sueco and 11 at Tinaja Verde. An increase in number of known territories as time progressed can be explained by increased survey area rather than change in number of existing pairs.

We began each annual survey prior to incubation and periodically observed pairs until fledging or failure was confirmed. To avoid overestimating productivity by overlooking pairs that failed early in the nesting season, we discounted pairs found late in the nestling period from our calculations of productivity (Steenhof 1987). In that regard, we did not calculate a productivity estimate from 1996 data, though we used them to estimate breeding chronology. We visited each occupied and previously occupied territory at least twice per month. In some cases, territories noted as unoccupied may have contained undetected pairs.

We observed nest contents with a mirror attached to a telescoping pole and estimated the age of nestlings by means of a photographic key (The Peregrine Fund unpubl. data). We used that information to calculate egg-laying and hatching dates on the basis of a 33-day incubation period, though a few start dates were directly observed. We calculated fledging rates using number of nestlings that reached 30 days of age. We marked 129 fledglings with federal bands and color VID bands. No physical evidence (e.g. predator tracks, scat, etc.) suggested an effect of monitoring on nest success, but we cannot rule out the possibility, because no nests were unvisited as controls (see Steenhof and Kochert 1982, Jenny et al. 2004).

PREY REMAINS COLLECTION

We collected prey remains at nests, below perches and plucking sites, during visits for reproduction monitoring at 26 territories during 2000–2002. We identified species by comparison with reference feathers. Small birds were under-represented in our collections to the extent that their remains were less persistent than those of larger birds. We did not estimate minimum numbers of individuals per collection by tabulating recurrence of like parts (Hunter et al. 1988), but instead compared the presence or absence of species remains per territory. Body mass of each species was obtained from Dunning (1993). Because only a minor portion of prey remains consisted of insects, we excluded them from the analysis.

BIRD SURVEY PLOTS

We counted birds from January 1998 to May 2002 using the area search plot method (Ralph et al. 1993). The surveyor began at a defined corner of each 3-ha plot and zig-zagged diagonally across it over a 20-min period, ending at the opposite corner. Birds detected during scanning were identified and counted. Timing of counts was set to cover the most important events in avian communities: wintering, spring migration, reproduction, and fall migration. We developed 65 count-plots in the vicinity of 11 Aplomado Falcon territories at Sueco and 65 plots in the vicinity of 8 territories at Tinaja Verde. Six habitat types were identified in aerial photographs (scale 1:35,000): shrubland, tobosa swale, barren slope, gramma grassland, savanna, and yucca grassland. Shrublands are areas with a high relative density of woody plants

<1.5 m in height, principally *F. cernua, L. tridentata, E. trifurca, Mimosa* spp., and *Acacia* spp. Tobosa swales are open grasslands dominated by *H. mutica*. Barren slopes are grassland areas disturbed by grazing, with bare ground and rocky and shallow soils, usually on hills, the most common vegetation being *Dasyochloa pulchella* and *B. eriopoda*. Gramma grasslands are those in relatively good condition, with little bare ground and a very low density of woody plants (shrubs); the main grasses occurring in that habitat are *Bouteloua* spp., *Aristida* spp., *Muhlenbergia* spp., and *Chloris* spp. Savannas are grasslands with low to moderate densities of woody vegetation, the most common species being *P. glandulosa, Mimosa* spp., *E. trifurca, Acacia* spp., *C. ericoides*, and *K. spinosa*. Yucca grasslands are savannas where yuccas, primarily *Yucca elata*, are the dominant woody vegetation. Number of plots assigned to each habitat type corresponded to relative area of each type in the two study areas.

We surveyed basal grass cover at each count plot during the dry seasons of 1998, 1999, and 2001. We counted and classified all woody plants into height classes (e.g. <1, 1–2, 2–3, and >3 m in 1998). We estimated basal grass cover using 100 sample points set systematically throughout the plot, as follows: a diagonal sampling base line originating from one corner and bisecting the plot was dissected into 10 sampling lines on alternating sides of the baseline at 22-m intervals.

To relate bird abundance with falcon reproduction, we considered only those species that were potential prey, the latter selected according to three criteria: (1) those species we found in prey remains, (2) those reported as prey in the literature, and (3) those <100 g. We estimated bird density per count at each study area by dividing number of birds detected in all plots by total area surveyed (i.e. 195 ha; 3 ha $plot^{-1} \times 65$ plots). We calculated mean density of birds during the falcon breeding season by averaging density estimates from January to May. We similarly averaged prey abundance in February and March to detect influence of prey abundance in the early breeding season. Both measures were subdivided into presence and weight classes. Presence classes were wintering, resident, breeding, and migrant; weight classes were <25, 25–50, 50–100, and >100 g. In the latter category, we did not consider Scaled Quail (*Callipepla squamata*), American Kestrel (*Falco sparverius*), and Greater Roadrunner (*Geococcyx californianus*) in our analysis, because of their rarity in prey remains and the skewing they impart to their weight class; Mourning Dove (*Zenaida macroura*) was the only remaining species weighing >100 g.

Statistical analyses

We used linear correlation analyses to examine relationships between Aplomado Falcon reproduction parameters and prey abundance indices. We used simple correlation analysis to identify patterns of habitat use by potential avian prey. We indexed species abundance at each plot required for the analysis by pooling avian count data during the Aplomado Falcon breeding season (January–May) in all years (1998–2002). Vegetation variables included woody plants <1, 1–2, 2–3, and >3 m, and percentage of basal grass cover (the average of 1998, 1999, and 2001 data). We subjected all correlation coefficients to a *t*-test of zero correlation (H_0: $\rho = 0$ vs. H_a: $\rho \neq 0$) (Daniel 1993). We performed Bonferroni adjustments to avoid random correlations (Rice 1989); to minimize type-II errors, we selected an α-value of 0.10 as statistically significant (Lehman et al. 2000).

Results

Clutch size at Sueco and Tinaja Verde was similar, at 2.82 ± 0.06 and 2.83 ± 0.10 eggs, respectively; and brood size was comparable at 2.19 ± 0.12 and 2.22 ± 0.32 fledglings per successful nest at the two study areas, respectively. Productivity differed, however: number of fledglings per occupied territory was significantly higher at Sueco (0.94 ± 0.12) than at Tinaja Verde (0.53 ± 0.17) ($t = 1.99$, df = 73, $P = 0.05$). That difference arose from significantly lower brood survival (proportion of nestlings that fledged, $z = 3.50$, $P = 0.0002$) at Tinaja Verde and not from the proportion of active pairs ($z = 0.83$, $P = 0.20$) or hatching rates (eggs laid that hatched, $z = 0.22$, $P = 0.41$). At Sueco, percentage of occupied territories that were active varied from 48% to 79% per year, though no significant trend over time was apparent ($r = -0.50$, $t = -1.15$, df = 4, $P = 0.31$). However, falcon productivity declined significantly during 1997–2002 ($r = -0.77$, $t = -2.45$, df = 4, $P = 0.07$; Fig. 3), which is consistent with a significant decline in proportion of occupied territories that were successful ($r = -0.87$, $t = -3.55$, df = 4, $P = 0.02$). Moreover, mean incubation start date showed a trend of delay from 1996 to 2001 ($r = 0.96$, $t = 7.25$, df = 4, $P = 0.002$), though that trend reversed direction in 2002 (Fig. 4), which is consistent with changes in prey bird numbers (see below).

We identified remains of 44 species in the prey remains of at least 458 individuals collected at 26 territories during 2000–2002. Overall, Mourning Doves (119 g), Northern Mockingbirds (49 g), and meadowlarks (95 g) were most frequently recorded (Fig. 5). Proportions of most prey taxa in remains were similar between the two study

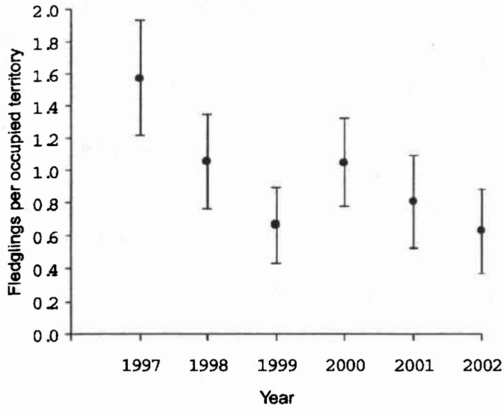

Fig. 3. Falcon reproduction at the Sueco study area during 1996–2002.

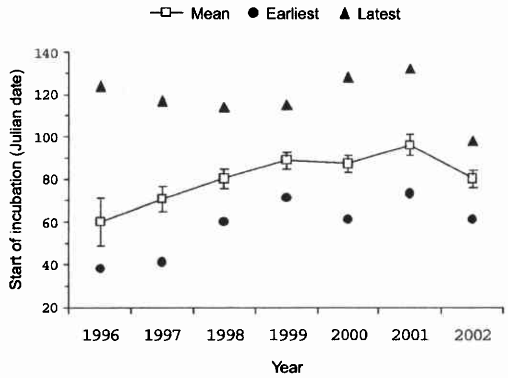

Fig. 4. Incubation start dates of Aplomado Falcons from 1996 to 2002.

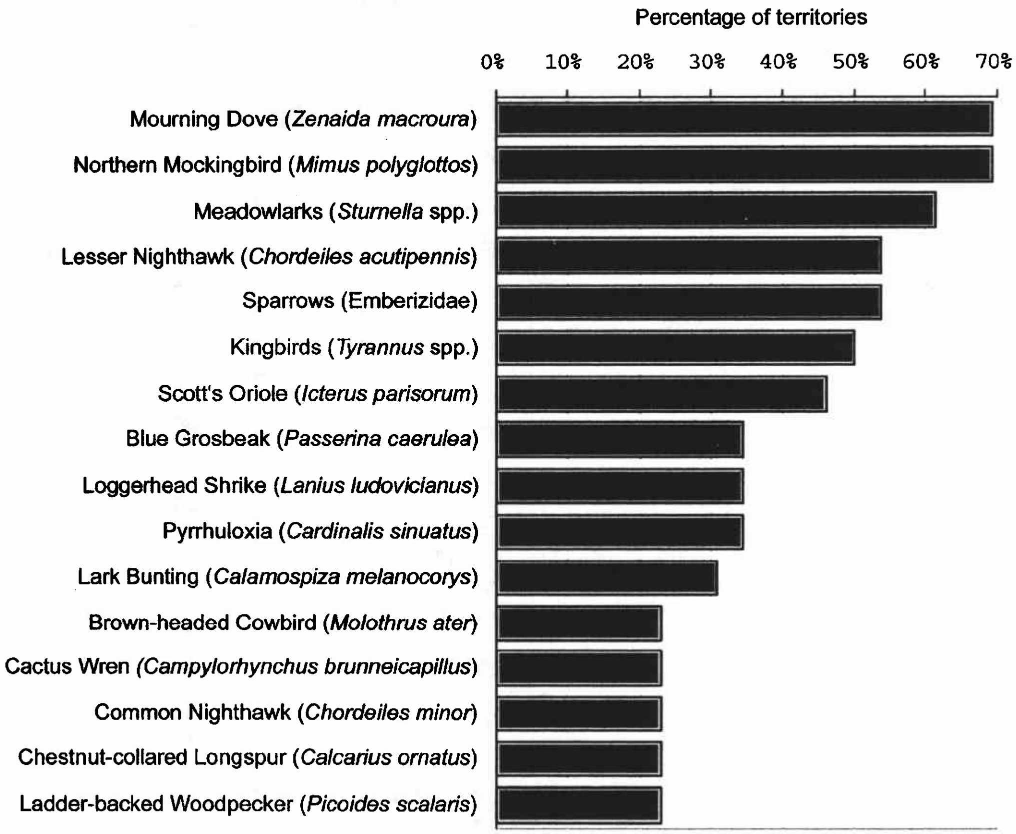

Fig. 5. Bird taxa found in Aplomado Falcon prey remains during the breeding seasons of 2000–2002 in Chihuahua. An additional 28 species not shown in the graph were identified at <20% of territories (Table 1).

areas; exceptions were that Mourning Doves appeared at a greater proportion of nests at Sueco than Tinaja Verde (75% vs. 50% of nests, respectively), whereas Blue Grosbeaks (25% vs. 67%), orioles (35% vs. 83%), and sparrows (65% vs. 100%) appeared less frequently. Table 1 lists all avian species identified in prey remains.

In avian prey surveys at Sueco, Horned Larks, Chestnut-collared Longspurs, Brewer's Sparrows, and meadowlarks accounted for >70% of relative biomass and >75% of relative abundance recorded in count plots during the breeding season (January–May). Species with highest aggregate biomass were those with body masses of <25 g (43.9%) at Sueco and 20–50 g at Tinaja Verde. Even though the relative abundance of birds >50 g at both study areas was <10%, that group accounted for a much

TABLE 1. Bird species present in prey remains of Aplomado Falcons in Chihuahua, Mexico.

Common name	Scientific name	Individual mass (g)
American Kestrel	*Falco sparverius*	115
Scaled Quail	*Callipepla squamata*	184
Virginia Rail	*Rallus limicola*	85
Sora	*Porzana carolina*	75
White-winged Dove	*Zenaida asiatica*	153
Mourning Dove	*Zenaida macroura*	119
Greater Roadrunner	*Geococcyx californianus*	376
Lesser Nighthawk	*Chordeiles acutipennis*	50
Common Nighthawk	*Chordeiles minor*	61
Common Poorwill	*Phalaenoptilus nuttallii*	50
Acorn Woodpecker	*Melanerpes formicivorus*	80
Ladder-backed Woodpecker	*Picoides scalaris*	30
Northern Flicker	*Colaptes auratus*	130
Say's Phoebe	*Sayornis saya*	21
Vermilion Flycatcher	*Pyrocephalus rubinus*	14
Ash-throated Flycatcher	*Myiarchus cinerascens*	27
Cassin's Kingbird	*Tyrannus vociferans*	46
Western Kingbird	*Tyrannus verticalis*	40
Loggerhead Shrike	*Lanius ludovicianus*	47
Western Scrub-Jay	*Aphelocoma californica*	85
Horned Lark	*Eremophila alpestris*	31
Cactus Wren	*Campylorhynchus brunneicapillus*	39
Black-tailed Gnatcatcher	*Polioptila melanura*	5
Northern Mockingbird	*Mimus polyglottos*	49
Mountain Bluebird	*Sialia currucoides*	30
American Pipit	*Anthus rubescens*	21
Sprague's Pipit	*Anthus spragueii*	25
Green-tailed Towhee	*Pipilo chlorurus*	29
Spotted Towhee	*Pipilo maculatus*	40
Brewer's Sparrow	*Spizella breweri*	11
Vesper Sparrow	*Pooecetes gramineus*	26
Lark Sparrow	*Chondestes grammacus*	29
Black-throated Sparrow	*Amphispiza bilineata*	13
Lark Bunting	*Calamospiza melanocorys*	38
Savannah Sparrow	*Passerculus sandwichensis*	19
Chestnut-collared Longspur	*Calcarius ornatus*	19
Pyrrhuloxia	*Cardinalis sinuatus*	35
Black-headed Grosbeak	*Pheucticus melanocephalus*	45
Blue Grosbeak	*Passerina caerulea*	28
Red-winged Blackbird	*Agelaius phoeniceus*	52
Eastern and Western meadowlarks	*Sturnella* spp.	95
Great-Tailed Grackle	*Quiscalus mexicanus*	149
Brown-headed Cowbird	*Molothrus ater*	44
Scott's Oriole	*Icterus parisorum*	37

larger proportion of the relative biomass (Table 2). At Tinaja Verde, Horned Larks, meadowlarks, Chestnut-collared Longspurs, and Black-throated Sparrows made up >70% of relative biomass and 68.3% of relative abundance.

Sueco and Tinaja Verde differed in overall bird abundance, largely because higher numbers of wintering birds were present at the former. At Sueco, wintering birds were more abundant than resident birds in the early falcon breeding season in all years except in 2001. Tinaja Verde had a similar mean density of resident birds (0.61 birds ha^{-1}) to Sueco (0.80 birds ha^{-1}; $t = 0.78$, df = 27, $P = 0.44$), but received significantly lower numbers of wintering birds (0.27 birds ha^{-1}) than Sueco (1.36 birds ha^{-1}; $t = 2.15$, df = 18, $P = 0.04$). However, the contribution of wintering birds to overall avian biomass during the falcon breeding season, despite their high abundance (Table 2), was relatively low, compared with that of resident birds (Fig. 6), because body masses of wintering birds (e.g. sparrows) tended to be lower than those of resident birds. Total biomass of resident birds was always higher than that of wintering birds at Tinaja Verde.

Number of fledgling Aplomado Falcons per occupied territory was positively correlated ($r = 0.97$) with mean number of prey weighing 50–100 g per count during the falcon breeding season (January–May; Fig. 7). Mean incubation start date was negatively correlated with abundance of resident birds ($r = -0.99$; Fig. 8) in the February and March–April counts (i.e. the higher the number of prey, the earlier Aplomado Falcons began nesting).

Significant correlations that arose in comparisons between prey bird abundance and grass cover and density of woody vegetation within the bird survey plots (Table 3) identify the importance of woody vegetation to many of the species identified as Aplomado Falcon prey. Some species, like nighthawks and kingbirds, do not appear in Table 3 despite their importance in the Aplomado Falcon diet (Montoya et al. 1997); they were encountered in the surveys

Table 2. Relative abundance and biomass during January–May of prey species recorded at 130 plots at Sueco and Tinaja Verde study areas from 1998 to 2002 ("w" indicates wintering species).

	Sueco		Tinaja Verde	
Species	Biomass (%)	Abundance (%)	Biomass (%)	Abundance (%)
	Weight <25 g			
Calcarius ornatus (w)	22.1	27.3	8.3	13.8
Spizella breweri (w)	12.9	27.6	3.1	9.0
Amphispiza bilineata	1.5	2.6	5.7	13.3
Unidentified sparrows	1.1	1.5	0.8	1.4
Spizella passerina (w)	1.1	2.0	0.1	0.3
Ammodramus spp. (w)	1.9	2.6	1.1	2.0
Passerculus sandwichensis (w)	0.9	1.1	0.6	1.0
Aimophila cassinii	0.9	1.1	2.0	3.3
Others	1.4	2.1	1.2	2.2
	43.9	**67.9**	**22.9**	**46.3**
	Weight 25–50 g			
Eremophila alpestris	25.5	19.0	31.9	31.9
Lanius ludovicianus	3.5	1.7	4.5	3.0
Pooecetes gramineus (w)	3.4	3.1	1.2	1.4
Campylorhynchus brunneicapillus	1.8	1.0	4.3	3.5
Mimus polyglottos	1.3	0.6	1.9	1.2
Anthus spragueii (w)	0.7	0.6	0.9	1.1
Others	3.2	2.1	1.8	1.6
	39.3	**28.1**	**46.4**	**43.7**
	Weight >50 g			
Sturnella spp.	12.1	3.0	28.18	9.3
Zenaida macroura	4.6	0.9	2.36	0.6
Toxostoma curvirostre	0.1	0.0	0.09	0.0
	16.8	**3.9**	**30.62**	**9.9**

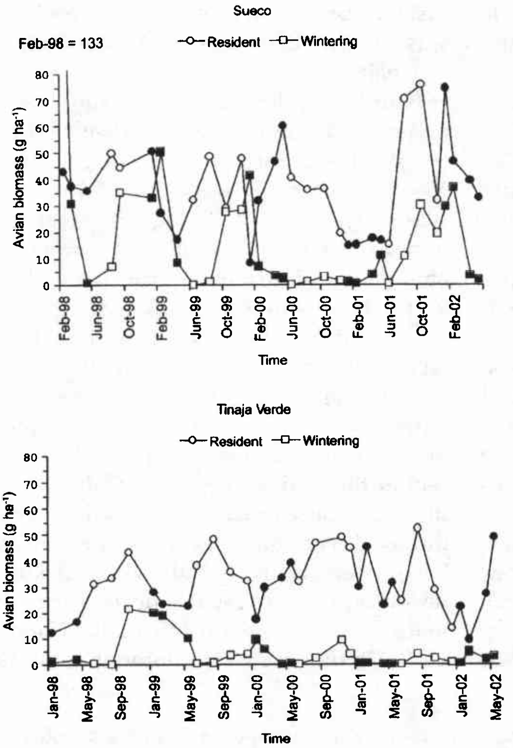

FIG. 6. Estimated biomass (g) of prey birds ha^{-1} at 130 study plots in the Sueco and Tinaja Verde study areas (1998–2002). Solid circles and squares are values for resident and wintering birds, respectively, recorded during the reproductive season (January–May); unfilled circles and squares are values for the rest of the year.

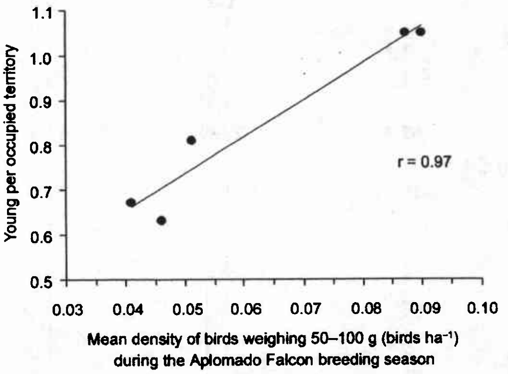

FIG. 7. Linear correlation between fledglings per occupied territory and mean monthly number of prey weighing 50–100 g, at Sueco study area. Each point in the plot corresponds to one year (1998–2002).

in very low numbers. The conspicuous absence of significant correlations between grass cover and grassland species, such as Horned Larks and Chestnut-collared Longspurs, may be related to flock approachability in the open landscape; both species showed negative correlations with woody plant density.

DISCUSSION

Drought may strongly affect bird abundance and demography in arid landscapes (Newton 1998). Hustler and Howells (1990) found that correlations between rainfall and reproductive success in several raptor species in Zimbabwe were explained by effects of primary production on consumers (prey populations); raptors raised fewer young and laid eggs at later dates in years of lower precipitation. Wichmann et al. (2003) modeled the effect of rainfall scenarios associated with climatic change on population persistence of the Tawny Eagle (*Aquila rapax*) in arid African savannas; extinction risk increased not only with reductions in mean precipitation values but also with changes in interannual variation (e.g. through autocorrelation and monotonic trends; see also Moss et al. 2001). Populations of medium-sized raptors, like the Aplomado Falcon, have also been shown to be strongly influenced by rainfall (Krüger et al. 2002).

Poor reproduction in Chihuahua is therefore expected in view of the severe drought conditions affecting the region since about 1992 (Fig. 1). Although we cannot directly examine the relationship of rainfall and reproduction, because our study began after the drought had been in progress for several years, the overall reproductive rate of 0.83 fledglings per occupied territory in Chihuahua during 1996–2002 (0.79 during 2000–2002) is far lower than that reported for several other falcon species, for example, 1.6 for Peregrine Falcons (*F. peregrinus*; White et al. 2002), 2.5 for Prairie Falcons (*F. mexicanus*; Steenhof 1998), and 3.6–3.8 for Merlins (*F. columbarius*; Sodhi et al. 1993). The only other population of Aplomado Falcons available for a comparison of reproduction is that currently being re-established in southern Texas. The rate in Texas was 1.2 during 2001–2002, but the recency of pair establishment (first noted in 1995) and age structure of the breeding segment may not accurately reflect the natural

Table 3. Significant correlations ($P < 0.10$) between abundance of recorded prey species (1998–2002) and habitat structure variables at Sueco and Tinaja Verde. The (+) and (–) are significant positive and negative correlations, respectively, and (++) and (– –) are significant correlations after Bonferroni adjustment. Asterisks mark species identified in falcon prey remains from >20% of nests.

		Density of woody plants			
Species	Grass cover	<1 m	1–2 m	2–3 m	>3 m
	Sueco				
Spizella breweri	– –		++	++	++
*Campylorhynchus brunneicapillus**	– –			++	++
Eremophila alpestris				–	
*Lanius ludovicianus**	– –			++	++
Sturnella spp.*	+				
*Zenaida macroura**					++
*Mimus polyglottos**	– –			++	++
	Tinaja Verde				
Spizella breweri	– –		+	+	
*Campylorhynchus brunneicapillus**			++	++	+
Eremophila alpestris	– –			– –	– –
*Lanius ludovicianus**				++	++
*Zenaida macroura**	– –	++	++		
*Mimus polyglottos**	– –	++	++	++	
*Icterus parisorum**				++	

state (Jenny et al. 2004). Keddy-Hector (2000) reported 1.5 fledglings per active nest in eastern Mexico during 1977–1986, but there was no estimate of fledglings per occupied territory.

The positive relationship between falcon reproduction and prey abundance (Fig. 7) supports the hypothesis of a causal influence of drought on prey availability. Jamus et al. (2003) found that drought in a Chihuahuan Desert grassland severely reduced numbers of Mourning Doves, a prey species of central importance to Aplomado Falcons in our study area (Fig. 5). The declining trend of reproduction is likely attributable to accumulative effects on those and other prey populations over consecutive years of below-average rainfall. Abundance data from our avian prey surveys suggest that relationship, but no clear trend is apparent in overall biomass (Fig. 6). Seed and insect production in Chihuahuan Desert grasslands are directly related to summer rainfall (Pulliam and Brand 1975, Dunning and Brown 1982); arthropod abundance is highest during the flush of vegetative biomass during late summer and dwindles in fall and winter (Whitford et al. 1995). Given that chronology, seed availability is likely more important than insect availability in determining prey abundance during the breeding season (Dunning and Brown 1982). It follows that the relationship between incubation start date and abundance of resident prey in February–April (Fig. 8) hinges on seed abundance during the early falcon season when insect densities are low. The most important birds that depend on seeds during that period are wintering sparrows, Mourning Doves, and meadowlarks (Lanyon 1994); whereas most of the insectivores important as Aplomado Falcon prey (Fig. 5) are either absent in winter or present in low numbers.

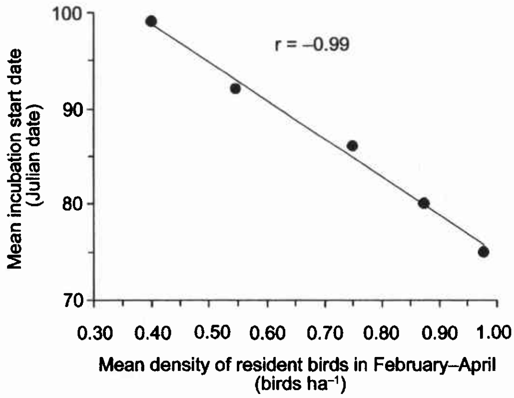

Fig. 8. Linear correlation between mean incubation start date and abundance of resident prey recorded in February and March–April counts at Sueco. Each point in the plot corresponds to one year (1998–2002).

The relationship we observed between prey abundance and incubation start date of the falcons (Fig. 8) is consistent with studies of other bird species (Hustler and Howells 1990, Newton 1998). A possible consequence of delayed nesting of Aplomado Falcons that may partly account for low productivity is increased competition for nest structures with Chihuahuan Ravens (*Corvus cryptoleucus*); that is, a later-than-normal falcon nesting season overlaps with that of ravens (Ligon 1961). We have observed ravens trying to occupy nests already selected by Aplomado Falcons, standing on active falcon nests while being attacked by the parents, and nesting in failed falcon nests. Moreover, drought-reduced prey abundance may force falcons to leave the nest area for extended periods to procure food, thereby increasing the risk of raven predation on eggs and nestlings. Not surprisingly, the ratio of lost broods to occupied territories in both study areas increased from 3% (1997–1999) to 16% (2000–2002) as prey bird numbers declined.

Despite higher average precipitation and lower overall grazing pressure at Tinaja Verde, reproduction was lower there than that at Sueco (0.53 vs. 0.94 fledglings per occupied territory, respectively). The lower densities of wintering prey birds recorded in surveys at Tinaja Verde may have influenced the physical condition of falcons in the early stages of breeding, though mean incubation start date between the two study areas was similar ($t = 0.06$, df = 25, $P = 0.95$). We have no clear explanation for the area difference in wintering bird densities. Tinaja Verde grasslands are more geographically insolated from other grassland areas and possibly from bird migration routes.

Our data suggest that, even though falcons almost invariably nested in areas of very sparse woody vegetative cover, proximity of shrublands may have been important (Table 3). Keddy-Hector (1986, 2000) hypothesized that ideal habitat for Aplomado Falcons in eastern Mexico consisted of "open savanna or grassland surrounded by or bordering extensive woodland or wetlands"—the suggestion being that, while prey birds are more abundant in woodland, they are more easily caught in the open landscape. Aplomado Falcons typically hunt from perches in the vicinity of the nest, where they presumably remain to deter nestling predation (Hector 1981). A nest in open grassland offers less escape cover to prey being pursued by falcons, and there are fewer Great Horned Owls (*Bubo virginianus*), the principal predator of Aplomado Falcons in Chihuahua (A. B. Montoya unpubl. data). However, abundance and biomass of important prey species are typically higher in shrublands than in grasslands (Lima and Valone 1991, Pidgeon et al. 2001, present study), a factor supporting Keddy-Hector's hypothesis that optimum nest placement is a compromise between the two.

However, the trend of widespread woody plant encroachment associated with overgrazing in the desert grasslands of the southwestern United States (Humphrey 1958, Buffington and Herbel 1965, Hastings and Turner 1965) clearly did not benefit Aplomado Falcons over the long term. Hector (1981) showed that Aplomado Falcons were intolerant of such encroachment in eastern Mexico in areas where leguminous brush had proliferated. In Chihuahua, that sensitivity is implied by the virtual absence of nests in locations of even moderate woody plant cover. Interestingly, desert grasslands in Chihuahua did not show extensive habitat modification until fairly recently (Enríquez 2001); the presence of Apache Indians in the late 1800s and the subsequent Mexican Revolution retarded water development and livestock numbers before 1940 (Enríquez 2001). That may explain why Aplomado Falcons remained in Chihuahua while they disappeared in the United States. Nowadays, desert grasslands in northern Mexico are undergoing desertification, largely as a consequence of overgrazing (Velazco-Molina 1991, Estrada Berg et al. 1999, Enríquez 2001, Parizek et al. 2002) and doubtless aggravated by the current drought. According to Breeding Bird Survey data, populations of grassland birds have, as a group, experienced steeper, more consistent, and more geographically widespread declines than any other behavioral or ecological guild (Samson and Knopf 1994, Peterjohn and Sauer 1999). The positive relationships in the present study between abundance of birds of 50–100 g and reproductive success and between number of resident birds and mean incubation start dates clearly indicate the importance of grassland bird conservation not only within the Chihuahuan Desert but also in the northern prairies where many of those species breed.

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