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BREEDING BIOLOGY AND NEST-SITE SELECTION OF RED-TAILED HAWKS IN AN ALTERED DESERT GRASSLAND

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ABSTRACT.—Red-tailed Hawks (*Buteo jamaicensis*) have expanded their range as trees have invaded formerly-open grasslands. Desert grasslands of southern Arizona have been invaded by mesquite trees (*Prosopis velutina*) since Anglo-American settlement and now support a large population of Red-tailed Hawks. We studied a population of Red-tailed Hawks in an altered desert grassland in southern Arizona. Our objectives were to determine what environmental characteristics influence Red-tailed Hawk habitat selection in mesquite-invaded desert grasslands and to evaluate the habitat quality of these grasslands for Red-tailed Hawks based on nesting density, nest success, and productivity. Red-tailed Hawks had 86% (95% C.I. = 73–99) nest success and 1.82 young per breeding pair (95% C.I. = 1.41–2.23). Nesting density was 0.15 (95% CI = 0.08–0.21) breeding pairs/km^2 and the mean nearest-neighbor distance was 1.95 km (95% C.I. = 1.74–2.16). Red-tailed Hawks selected nest-sites with taller nest-trees and greater tree height and cover than were available at random. Mesquite trees in desert grasslands provide abundant potential nesting structures for Red-tailed Hawks.

KEY WORDS: *Red-tailed Hawks*; Buteo jamaicensis; *desert grasslands*; *breeding biology*; *habitat selection*; *Arizona.*

BIOLOGÍA REPRODUCTIVA Y SELECCIÓN DE SITIOS DE NIDIFICACIÓN DE *BUTEO JAMAICENSIS* EN PASTIZALES DESÉRTICOS ALTERADOS

RESUMEN.—Los halcones de la especie *Buteo jamaicensis* han expandido su rango de distribución debido a la invasión de árboles en lo que en el pasado eran pastizales abiertos. Desde los asentamientos del hombre Anglo-Americano, los pastizales desérticos del sur de Arizona han sido invadidos por *Prosopis velutina*, y actualmente estos pastizales mantienen una gran población de *B. jamaicensis*. Estudiamos una población de *B. jamaicensis* en un pastizal desértico modificado en el sur de Arizona. Nuestros objetivos fueron determinar que tipo de características ambientales influencian la selección de hábitat de *B. jamaicensis* en los pastizales desérticos invadidos por *P. velutina* y evaluar la calidad del hábitat de estos pastizales para *B. jamaicensis*, basándonos en la densidad de sitios de nidificación, el éxito reproductivo y la productividad. Los individuos de *B. jamaicensis* tuvieron un 86% (95% IC = 73–99) de éxito de nidificación y produjeron 1.82 juveniles (95% IC = 1.41–2.23) por pareja reproductiva. La densidad de sitios de nidificación fue de 0.15 (95% IC = 0.08–0.21) parejas reproductivas/km^2 y la distancia promedio mínima al vecino más cercano fue de 1.95 km (95% IC = 1.74–2.16). *B. jamaicensis* seleccionó sitios de nidificación con árboles más altos y con un mayor volumen de vegetación que en sitios elegidos al azar. Los árboles de *P. velutina* proveen abundantes estructuras potenciales de nidificación para *B. jamaicensis* en los pastizales de desierto.
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The Red-tailed Hawk (*Buteo jamaicensis*) has been characterized as a relatively open-habitat hawk that requires a few trees for perch and nest sites (Bednarz and Dinsmore 1982, Preston and Beane 1993). Prior to the introduction of grazing and fire suppression by Anglo-American settlers in the late 1800s, desert grasslands in the southwestern United States were relatively treeless (Bahre 1995, McClaran 1995, 2003). In the roughly 100 years following the introduction of grazing and fire suppression, mesquite trees (*Prosopis velutina*) have invaded desert grasslands, transforming them into mesquite-grass savannas (Bahre 1995, McClaran 1995, 2003). In other grasslands throughout the western United States where grazing and fire suppression have supported the establishment of trees over the last century, Red-tailed Hawks have extended their range or become more common (Gilmer et al. 1983, Houston and Bechard 1983, Preston and Beane 1993). Although invasion of other grasslands by trees has allowed Red-tailed Hawks to expand their range, the effects of mesquite invasion on Red-tailed Hawk populations living in desert grasslands are unknown.

In the Sonoran desert scrub of southern Arizona, Red-tailed Hawks nest exclusively in saguaro cactus (*Carnegiea gigantea*; Mader 1978), despite the presence of trees such as paloverde (*Cercidium* spp.) and ironwood (*Olneya tesota*). Red-tailed Hawks may be inhibited from nesting in paloverde and ironwood because of their dense canopy structure (Mader 1978). Importantly, saguaro densities are low in desert grasslands. If Red-tailed Hawks are inhibited from using mesquite, as they are paloverde and ironwood, nest sites may be limiting in desert grasslands despite the abundance of mesquite.

We studied a Red-tailed Hawk population in the desert grasslands of southern Arizona. Our objectives were to determine what environmental characteristics may influence Red-tailed Hawk habitat selection in mesquite-invaded desert grasslands and to evaluate the habitat quality of these grasslands for Red-tailed Hawks by comparing their density, nest success, and productivity in this environment to the results of Red-tailed Hawk studies in other environments.

Methods

Study Area. The study area was a 100-km^2 area of desert grassland located on the University of Arizona's Santa Rita Experimental Range (SRER), which is about 40-km south of Tucson in Pima County, Arizona (McClaran 1995). Red-tailed Hawks were the most common large raptor on the SRER, but Swainson's Hawks (*B. swainsoni*) and Great Horned Owls (*Bubo virginianus*) were also present.

The SRER is located between 900–1300 m elevation on gently sloping alluvial fans bisected by drainages. It receives 250–500 mm of rain per year with over half the annual rain falling between July and September (Anable 1989). Mean daily temperature is approximately 11.6°C in the winter (October–March) and 21.8°C in the summer (April–September; NCDC 2004).

Desert grasslands in Arizona form a perennial grass-scrub dominated landscape transitioning into desertscrub at lower elevations and oak-pine woodlands at higher elevations (Brown 1994). Since the late 19th century, desert grasslands on the SRER have been invaded by mesquite, shrubs, cacti, and non-native grasses, creating a mesquite-Lehman lovegrass (*Eragrostis lehmanniana*) savanna (Medina 1996, McClaran 2003). However, ''desert grassland'' is accepted nomenclature for the mixture of vegetation found on the SRER, and we use this term throughout this paper (McClaren and Van Devender 1995).

Nest Searches. We used walking and driving surveys between April–July of 1999 to search the study area for nests of large raptors (Fuller and Mosher 1987). We drove all roads on the study area at 15–25 kph (130 km) and walked all non-roaded areas on foot (193 km).

We used a hand-held Global Positioning System (GPS) receiver to record the coordinates of nests that we found and identified which nests were occupied by breeding Red-tailed Hawks. Pairs were considered breeding if eggs, young, or incubating adults were present during a nest check (Steenhof 1987). In April 2001, we revisited all old stick nests located in 1999 to determine which nests were occupied by breeding Red-tailed Hawks.

Nest Success and Productivity. We checked all occupied nests every 10–14 d to determine nesting status and number of young fledged. Nests were checked with a spotting scope from >50 m away whenever possible to reduce disturbance to nesting hawks.

We calculated both apparent and Mayfield nest success to facilitate comparisons with other studies (Mayfield 1975, Hensler and Nichols 1981). We calculated apparent nest success as the number of successful nests divided by the number of nests with breeding pairs and used a 78-d nesting period for Mayfield calculations (Nice 1954, Preston and Beane 1993). Nest check intervals <15 d seem to be sufficient for determining nest success of raptors without violating the assumptions of the Mayfield method (Johnson 1979).

Productivity was measured as the number of young fledged per successful pair and per breeding pair (Minor et al. 1993). A breeding pair was considered successful if at least 1 young was in the nest at 80% of fledging age (≥37 d; Steenhof and Kochert 1982). Fledge or fail dates were assumed to be the midpoint between the last visit in which young were recorded in the nest and the next visit when no young were present (Mayfield 1975).

Nest-site Selection. To examine nest-site selection, we recorded vegetation characteristics within a circular plot of 11.3 m radius (0.04 ha) at nest-sites (N = 20) and randomly selected locations (N = 30). Random points were selected from a grid of potential points 100 m apart covering the entire study area; 15 random points were

Table 1. Means ± SE of characteristics measured at Red-tailed Hawk nest sites and random locations on the Santa Rita experimental Range, Arizona, in 1999 and 2001.

CHARACTERISTIC	RED-TAILED HAWK	RANDOM	F[b]	P[b]
N	20	30	—	—
Nest-tree height (m)	7.1[a] ± 0.4	3.8 ± 0.2	72.3	<0.001
Nest height (m)	5.6 ± 0.5	—	—	—
Mean tree height (m)	4.5 ± 0.2	3.8 ± 0.2	7.9	0.007
Tree cover (%)	22.9 ± 2.4	16.5 ± 1.9	4.5	0.039
Tree count	4.7 ± 0.8	3.7 ± 0.6	1.3	0.266
Elevation (m)	1132.5 ± 23.0	1135.6 ± 16.8	0.0	0.911

[a] Mean includes wood power poles that served as nest support structures. Results for tree nest support structures only are: $\bar{x} = 6.4 \pm 0.2$; $F = 64.1$; $P < 0.001$; $N = 17$.
[b] One-way Analysis of Variance.

selected from this grid for each year of the study. Nest-sites that were sampled in 1999 ($N = 14$) were not sampled again in 2001, even if they were occupied in both years. Because we did not mark individual birds, however, different nests within the same territory may have been measured in both years.

Nest-site plots were centered on the nest tree, and random plots were centered on the nearest tree (≥2.5 m in height) to the preselected coordinate. Woody plants ≥2.5 m tall were considered to be trees. Wood power poles were included as potential center points for random plots because they were used as nesting structures by Red-tailed Hawks, but no random plots were centered on power poles because a power pole was never the closest potential nesting structure to a randomly-selected coordinate.

We recorded the height of all nests and the species and height for nest trees and random trees. Power poles that served as nesting structures were treated the same as nest trees. We measured the following variables at both nest-site plots and randomly-selected plots: mean height of trees; percent canopy cover of trees; number of trees on the plot; and elevation of the plot. Height and cover were estimated visually. Height estimates were facilitated by the use of a 3-m measuring pole. Elevations were obtained from a 30-m Digital Elevation Model (DEM) by sampling elevation at nest-site and random plot locations using ArcInfo GIS software version 7.2.1 (ESRI 1998).

We used Fisher's Exact Test to assess differences in nest success between years and a t-test to assess differences in nearest-neighbor distances between years. We used stepwise logistic regression with $P = 0.25$ to enter and $P = 0.10$ to remove to assess the effects of environmental variables on nest-site selection (nest sites versus random sites). Logistic regression analyses were run in SYSTAT Version 9.0 (SPSS 1998). All other statistical analyses were run in SPSS Version 10.0.5 (SPSS 1999). Before building the logistic regression model, we used Pearson correlation analyses to check for variables with correlations ≥0.7, but no variables had correlation values of ≥0.7.

RESULTS

Nest Success and Productivity. We located 14 breeding pairs in 1999 and 15 in 2001. Data for one nest from 1999 were excluded from calculations of nest success and productivity because we did not know the fate of the nest. Nine (64%) of the nests occupied in 1999 were also occupied in 2001. Red-tailed Hawks averaged 86% (95% C.I. = 73–99%) nest success and 1.82 (95% C.I. = 1.41–2.23) young per breeding pair over the course of the study. Nest success was similar between years ($P = 0.60$, Fisher's Exact Test, two-sided; Table 2).

Density and Nearest-neighbor Distances. Nesting density of breeding pairs was 0.14 (95% C.I. = 0–0.32) per km² in 1999 and 0.15 (95% C.I. = 0–0.33) in 2001. Mean nearest-neighbor distance was 1896 m (95% C.I. = 1542–2251) in 1999, 2006 m (95% C.I. = 1722–2290) in 2001, and 1953 m (95% C.I. = 1742–2164) for both years combined. There

Table 2. Mean nest success and productivity (95% Confidence Intervals) recorded for Red-tailed Hawks on the Santa Rita Experimental Range, Arizona, in 1999 and 2001.

		NEST SUCCESS (%)		NO. OF YOUNG FLEDGED	
YEAR	N	MAYFIELD	APPARENT	PER SUCCESSFUL PAIR	PER BREEDING PAIR
1999	13	82 (55–100)	92 (76–100)	2.08 (1.66–2.51)	1.92 (1.40–2.44)
2001	15	66 (40–100)	80 (60–100)	2.17 (1.57–2.76)	1.73 (1.06–2.41)
All	28	72 (52–100)	86 (73–99)	2.13 (1.79–2.46)	1.82 (1.41–2.23)

Table 3. Red-tailed Hawk nest success and productivity reported in the literature.

AUTHOR	NEST SUCCESS (%)	YOUNG PER SUCCESSFUL PAIR	YOUNG PER BREEDING PAIR	LOCATION[a]
Moorman et al. 1999	67	—	0.84	Non-desert
Seidensticker and Reynolds 1971	50	1.70	0.90	Non-desert
Gates 1972	65	1.80	1.10	Non-desert
Minor et al. 1993	68	1.67	1.10	Non-desert
Kirkley and Springer 1980	66	1.96	1.29	Non-desert
Orians and Kuhlman 1956	77	1.93	1.43	Non-desert
Stout et al. 1998	82	1.75	1.43	Non-desert
Hansen and Flake 1995	72	2.00	1.47	Non-desert
Peterson 1979	81	1.80	1.50	Non-desert
Smith and Murphy 1979	88	1.70	1.50	Desert
Gilmer et al. 1983	72	—	1.52	Non-desert
Mader 1978	81	1.91	1.55	Desert
Johnson 1975	60	2.55	1.57	Non-desert
Restani 1991	—	—	1.65	Non-desert
This study	86	2.13	1.82	Desert
Hagar 1957	59	1.90	—	Non-desert
Steenhof et al. 1993	59	—	—	Non-desert

[a] Non-desert = study site not in a desert of the southwestern United States; Desert = study site in a desert of the southwestern United States.

was no difference in nearest-neighbor distances between years ($t_{27} = 0.52$, $P = 0.61$). Actual nearest-neighbor distances could be smaller than those reported because nests adjacent to the periphery of the study area could be closer than nests within the study area. When nests less than the nearest-neighbor distance from the boundary of our study area (1896 m for 1999, 2006 m for 2001) were removed, only nine nests remained. Mean nearest-neighbor distance for these nine nests was 2051 m (95% C.I. = 1829–2274), but the sample size was small.

Nest-tree Characteristics. Red-tailed Hawks nested most frequently in mesquite trees ($N = 16$, 80%), but also nested on wood power pole cross-bars ($N = 3$, 15%) and in Mexican blue oak (*Quercus oblongifolia*; $N = 1$, 5%). Nest trees were taller than randomly-selected trees (Table 1). The odds of a tree being a nest tree rather than a random tree on the landscape increased 9.69 (95% C.I. = 2.49–37.69) times for each m increase in tree height ($t_{48} = 3.28$, $P = 0.001$). We ran this analysis including and excluding power poles that served as nest support structures. The results were the same for both analyses.

Nest-site Characteristics. The mean height of trees on a plot was greater at nest sites than at random sites (Table 1). The odds of a plot being a nest site rather than a random site increased 2.35 (95% C.I. = 1.18–4.67) times for each m increase in tree height ($t_{48} = 2.44$, $P = 0.02$). No other variables in the logistic regression model explained differences between nest and random sites ($\chi^2_1 \leq 2.47$, $P \geq 0.12$). However, both mean tree height and percent cover of trees were greater at nest sites than random sites in a univariate analysis (Table 1).

DISCUSSION

Nest Success and Productivity. The nest success (86%, Table 2) and productivity (2.13 young/successful pair, 1.82 young/breeding pair; Table 2) that we observed on our study site were toward the upper end of the ranges of nest success and productivity reported in the literature for Red-tailed Hawks (Table 3). Other studies in southwestern deserts have also found relatively high nest success and productivity. In the desert scrub of Arizona, which is located lower in elevation than the grasslands of the SRER, nest success for a 3-yr period (1974–76) was 81% (Range = 71–93%), and mean productivity per breeding pair was 1.55 (Range = 1.36–1.79; Mader 1978). The productivity that we observed suggests adequate reproductive success for population stability (Henny and Wight 1969), but we did not collect data on other factors that may influence population dynamics, such as juvenile or adult survivorship or the number of territorial pairs that failed to breed.

Nest-tree Characteristics. The nest heights and nest-tree heights that we measured are among the lowest reported in the literature (Mader 1978, Schmutz et al. 1980, Hansen and Flake 1995). This is probably a result of the structural composition of desert vegetation. Mesquite trees, the primary nest-support structures on our study site, rarely grow more than 10 m tall. Red-tailed Hawk nest and nest-tree mean heights (6.6 m and 8.4 m, respectively) in the saguaro-paloverde flatlands of Arizona are also among the lowest reported in the literature (Mader 1978).

Red-tailed Hawks in saguaro-paloverde flatlands used saguaros exclusively for nest structures, despite the presence of ironwood and paloverde trees (Mader 1978). This may be because Red-tailed Hawks have difficulty penetrating and constructing nests in the canopies of ironwood and paloverde trees (Mader 1978). Bednarz and Dinsmore (1982) suggest that accessability is the overriding factor in tree nest-site selection by Red-tailed Hawks. Mesquites were the most commonly used (80%) nest support structures on our study site. Frequent use of mesquites as nest support structures, in conjunction with the high reproductive success that we observed, suggests that canopies of mesquite trees provided sufficient accessability for Red-tailed Hawk nesting.

Although it is possible that canopy structure could inhibit Red-tailed Hawks from nesting in some tree species, we believe that the height and availability of trees generally determines selection, rather than tree species (Petersen 1979). This means that the most conspicuous trees on the landscape tend to be the most common nest trees for Red-tailed Hawks. On our site, mesquites tended to be the largest, most abundant trees and were used most frequently as nest trees. In the saguaro-paloverde flatlands, saguaros are the most conspicuous (tallest) potential nest structures and provided the nest support structures for all Red-tailed Hawk nests (N = 35) located in that vegetation type during a 3-yr study (Mader 1978). Despite the presence of saguaros scattered sparsely throughout portions of our study site, no Red-tailed Hawks in our study nested in saguaros. In the few locations on our study site where saguaros occurred, mesquite tree branches capable of supporting Red-tailed Hawk nests tended to be higher than nearby saguaro cactus cross-arms, which could be used as nest support structures.

Nest-site Characteristics. Red-tailed Hawk nest-site characteristics vary widely with vegetation and topography (Preston and Beane 1993). Our results indicate that nest-sites of Red-tailed Hawks in desert grasslands of southern Arizona had greater tree height and canopy cover at nest sites than randomly selected plots, although tree height appeared to explain the differences between nest sites and random sites better than tree cover. Greater tree height and canopy cover may offer some potential benefits to nesting Red-tailed Hawks such as protection of the nest from strong winds or concealment from some types of predators. Newton (1979) suggests that a thick nest-tree crown may conceal the nest from below. Thick canopies on trees immediately surrounding the nest tree would enhance this function. Alternatively, greater tree height and cover at nest sites in this environment may simply be a result of the soil moisture conditions present at sites capable of producing trees of sufficient height to be selected as Red-tailed Hawk nesting substrates.

Density and Nearest-neighbor Distances. Red-tailed Hawk density and nearest-neighbor distances were well within the range of values reported in the literature (Table 4).

Habitat Quality and Response to an Altered Environment. Density alone is not a reliable indicator of habitat quality (Van Horne 1983), but the high reproductive success recorded for Red-tailed Hawks in this study in conjunction with moderate nesting densities and nearest-neighbor distances (Table 4) suggest that mesquite-invaded desert grasslands provide high quality habitat for Red-tailed Hawks. In fact, the invasion of desert grassland by mesquite cover over the last century has likely improved the habitat quality of desert grasslands for Red-tailed Hawks by increasing the availability and dispersion of nest sites and hunting perches. Unlike paloverde and ironwood trees in the saguaro-paloverde flatlands of Arizona, mesquite trees on the SRER did not appear to inhibit the ability of Red-tailed Hawks to penetrate and construct nests in their canopies. Therefore, the spread of mesquite into formerly open grasslands following the introduction of grazing and fire suppression has resulted in an increase in the availability and dispersion of potential nest support structures. Mesquite were the most commonly-selected nest trees (80%) on our study site.

Mesquite invasion of desert grasslands has also likely increased the habitat quality of desert grasslands by increasing the availability and dispersion of Red-tailed Hawk hunting perches. Several studies

Table 4. Red-tailed Hawk densities, listed from lowest to highest, found in the literature.

AUTHOR	DENSITY[a]	MEAN NEAREST-NEIGHBOR DISTANCE (km)	YEARS	STATE/PROVINCE	COUNTRY
Gilmer et al. 1983	0.005	—	3	ND	U.S.A.
Bosakowski et al. 1996	0.080	2.830	2	UT	U.S.A.
Minor et al. 1993	0.080	—	10	NY	U.S.A.
Gates 1972	0.094	—	3	WI	U.S.A.
Johnson 1975	0.125	—	2	MT	U.S.A.
McInvaille and Keith 1974	0.125	2.092	6	AB	Canada
Orians and Kuhlman 1956	0.135	—	3	WI	U.S.A.
This study	0.145	1.953	2	AZ	U.S.A.
Kirkley and Springer 1980	0.161	1.500	1	OH	U.S.A.
Hagar 1957	0.176	1.770	2	NY	U.S.A.
Peterson 1979	0.215	—	4	WI	U.S.A.
Runyan 1987	0.278	—	7	BC	Canada
Rothfels and Lein 1983	0.445	0.876	2	AB	Canada
Seidensticker and Reynolds 1971	—	2.092	2	MT	U.S.A.
Bechard et al. 1990	—	2.100	6	WA	U.S.A.
Smith and Murphy 1973	—	3.298	4	UT	U.S.A.

[a] Nesting pairs/km^2.

have found that raptor reproductive success is strongly affected by prey abundance (Southern 1970, Smith et al. 1981, James 1984). We did not measure prey abundance as part of this study, but it is likely that prey abundance was high during the course of our study, given the high reproductive success observed (Table 2). However, habitat quality for raptors is dependent on the vulnerability or accessibility of prey rather than on the abundance of prey alone (Baker and Brooks 1981, Preston 1990). Red-tailed Hawks are primarily perch hunters (Preston and Beane 1993), and their reproductive success seems to be influenced by the presence of a minimum number of well-dispersed perches within their territories (James 1984). When perches within Red-tailed Hawk territories are scarce and not well-dispersed, prey may be depleted near hunting perches while remaining relatively unexploited elsewhere (Kimball et al. 1970, James 1984). Mesquite were commonly used for perches by Red-tailed Hawks on the SRER. Thus, by increasing the availability and dispersion of hunting perches, mesquite invasion has likely increased access to prey resources for Red-tailed Hawks occupying desert grasslands in the Southwest.

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