



NEST-SITE CHARACTERISTICS AFFECT DAILY NEST-SURVIVAL RATES OF NORTHERN APLOMADO FALCONS (*FALCO FEMORALIS SEPTENTRIONALIS*)

JESSI L. BROWN,^{1,3} AND MICHAEL W. COLLOPY^{1,2}

¹Department of Natural Resources and Environmental Science, University of Nevada, 1000 Valley Road, Reno, Nevada 89512, USA;
and ²Academy for the Environment, University of Nevada, 108 Mackay Science Building, Reno, Nevada 89557, USA

ABSTRACT.—We modeled daily nest-survival rates (DSR) of a reintroduced population of Northern Aplomado Falcons (*Falco femoralis septentrionalis*; hereafter “falcons”) in southern Texas. Although falcons have nested in the region since 1995, the factors influencing reproductive success are not understood. Nest sites were classified into nest-type groups using a cluster analysis based on nest substrate and nest builder. Using an information-theoretic approach, we compared relative effects of nest age, study area, nest-type group, and physical nest-site characteristics. Our results were similar to previous studies of passerine nesting ecology, in that DSR varied throughout the nesting cycle: it was constant during incubation, declined at hatching and the early nestling phase, and increased through the remainder of the nestling phase. Nest type and nest height were important physical nest-site covariates, overhead cover was less important, and study area and nest initiation date were not influential. We note that although nest success was well correlated with simple nest-site covariates, many falcons chose poor-quality nest sites, which raises the question of whether nest-site selection by falcons is optimal in this region. Received 14 September 2006, accepted 14 March 2007.

Key words: Aplomado Falcon, *Falco femoralis*, nest survival, program MARK, raptor, reintroduction.

Las Características de los Sitios de Nidificación Afectan las Tasas de Supervivencia Diaria de los Nidos de *Falco femoralis septentrionalis*

RESUMEN.—Modelamos las tasas de supervivencia diaria de los nidos (TSD) de una población reintroducida de halcones *Falco femoralis septentrionalis* en el sur de Texas. Aunque los halcones han nidificado en la región desde 1995, no se conocen los factores que influyen el éxito reproductivo. Los sitios de nidificación fueron clasificados en grupos de tipos de nido usando un análisis de agrupamiento basado en el sustrato del nido y en el constructor del nido. Usando un enfoque de la teoría de la información, comparamos los efectos relativos de la edad del nido, el área de estudio, el grupo de tipo de nido y las características físicas del sitio de nidificación. Nuestros resultados fueron similares a los de estudios previos sobre la ecología de nidificación de los paserinos, en que la TSD varió a lo largo del ciclo de nidificación: fue constante durante la incubación, disminuyó en la eclosión y la etapa temprana de cría de pichones y aumentó a lo largo del resto de la fase de cría de pichones. El tipo de nido y la altura del nido fueron covariables físicas importantes del sitio de nidificación, la cobertura por encima del nido fue menos importante, y el área de estudio y la fecha de iniciación del nido no tuvieron influencia. Notamos que aunque el éxito de nidificación estuvo bien correlacionado con covariables simples del sitio de nidificación, muchos halcones eligieron sitios de nidificación de baja calidad, lo que plantea la pregunta si la selección del sitio de nidificación por los halcones es óptima en esta región.

ALTHOUGH THE NORTHERN Aplomado Falcon (*Falco femoralis septentrionalis*; hereafter “falcon”) is the subject of a large-scale reintroduction effort, little is known about population regulation in this endangered species (Keddy-Hector 2000, Jenny et al. 2004). Annual survival of adult falcons in a reintroduced population was relatively high (annual survival rate of breeding adults: 0.910; 95% confidence interval [CI]: 0.750–0.988), which is consistent with a “slow” life-history strategy (Heppell et al. 2000, Brown et al. 2006). As one extreme of the “slow–fast” continuum of

life-history traits, “slow” life-history strategies include long life span, slow development, and low reproductive rate (Heppell et al. 2000, Ricklefs 2000, Ricklefs and Wikelski 2002). These life-history traits are generally represented by the estimated demographic parameters of adult survival rate, age at maturity, and fecundity rate (Sæther and Bakke 2000).

If we have correctly characterized the falcons, it is likely that the population growth rate (λ) is more affected by changes in adult survival rate than proportional changes in fecundity;

³E-mail: jlbrown@unr.edu

more specifically, sensitivity to fecundity should be low, whereas sensitivity to adult survival should be high (Sæther and Bakke 2000). We could expect that "slow" species would experience greater pressure to evolve behavioral or physiological traits to maximize adult survival than to maximize annual productivity (Roff 2002). Therefore, we might find trade-offs between survival and reproduction, such that falcons would be present in habitats well suited for adult survival, even if the best nest sites available were of relatively poor quality. If falcons are not preferentially selecting the highest-quality nest sites, we may question whether they have the ability to evaluate nest-site quality (Martin 1995, Pöysä et al. 2001).

We analyzed daily nest-survival rates (DSR) for two populations of falcons in southern Texas. Our primary goal was to evaluate potential influences on nest success so that high-quality nests could be distinguished from lower-quality nests, thus providing a necessary precursor for determining whether nest-site selection by falcons maximizes fecundity. Captive-bred falcons, released as part of a reintroduction project beginning in 1993 and directed by The Peregrine Fund, rapidly established a wild breeding population (Jenny et al. 2004). The number of known breeding pairs, consisting of both captive-bred and wild-fledged descendants, increased throughout the 1990s until temporarily stabilizing at 38 pairs by 2002 (Peregrine Fund unpubl. data). We monitored falcon nesting attempts during 2002–2004. Data summarizing nest attempts were analyzed using the nest-survival model in MARK to assess relative influences of continuous, categorical, and time-varying factors (Dinsmore 2002).

METHODS

Study site.—We monitored territorial falcons in two study areas ~300 km apart in coastal southern Texas. Both sites, previously focal areas for reintroduction, are coastal savannah with generally low vegetation with few widely interspersed shrubs, but some aspects of species composition and community structure differ. The southwestern area, centered on Laguna Atascosa National Wildlife Refuge (NWR; 26°5'N, 97°21'W), is a patchwork of native Tamaulipan biotic-province landscapes, row-crop agriculture, suburban and urban development, and industry (Jahrsdoerfer and Leslie 1988). Falcons are restricted to remnant patches of coastal plains within refuge holdings as well as private cattle ranches. Honey Mesquite (*Prosopis glandulosa*), Granjeno (*Celtis pallida*), and Lime Pricklyash (*Zanthoxylum fagara*) are the most common trees, Spanish Dagger Yuccas (*Yucca treculeana*) are abundant, and low areas are carpeted with salt-tolerant species such as shoregrass (*Monanthochloe littoralis*), Maritime Saltwort (*Batis maritima*), Virginia Glasswort (*Salicornia virginica*), Sea Oxeye (*Borrchia frutescens*), and Gulf Cordgrass (*Spartina spartinae*; Perez et al. 1996).

The northeastern area, Matagorda Island NWR (28°14'N, 96°37'W), is a low barrier island along the Texas coastal bend. Its sandy dunes form an uneven topography that differs from the flat inland coastal plain. Trees and shrubs, mostly mesquite, Yaupon (*Ilex vomitoria*), and McCartney Rose (*Rosa bracteata*), are few and stunted, and yuccas are nearly absent (McAlister and McAlister 1993). However, in most areas, grasses and sedges

formed a thick mat of undergrowth that was managed through frequent controlled burns during the study.

Monitoring falcon pairs.—From January through July of each year, we systematically searched traditional territories until we found and identified the resident falcons by visual inspection of their leg bands. All captive-bred falcons (>800 individuals) were banded before release with U.S. Geological Survey (USGS) bands and, since 1998, colored aluminum visual identification (VID) bands with unique alphanumeric characters on the opposite tarsus. Wild-reared chicks in accessible nests were also banded with USGS and VID bands during 1995–2003 ($n = 108$). Because we were concerned with potential effects of observers on breeding activities, nearly all pairs were identified before the onset of courtship behavior, so that subsequently we could observe activity from a distance. Most nests were monitored from initiation (onset of incubation), because falcons were conspicuously active at their chosen nest site one to four weeks before egg laying, which simplified nest searching. We visited nests weekly, and more frequently when changes in nest status (i.e., hatching or fledging) were anticipated. During monitoring bouts, we watched nests until nest status could be determined (typically 15 min to 1 h). Nest age was determined by parental behavior or by aging nestlings using a photographic guide to chick development in captive-bred falcons (Peregrine Fund unpubl. data). With few exceptions, we approached nests only to band nestlings. Nests were deemed "successful" when one or more nestlings were confirmed to have fledged.

Nest-site measurements.—We measured nest-site characteristics either while banding nestlings or within two weeks following fledging or nest failure. Nest substrates were noted and tree–shrub species recorded if applicable. Potential nest substrates were either artificial or natural. Artificial nests could be "barred" nests, which are fully enclosed, with sides constructed of conduit spaced to permit passage of falcons, or "platform" nests, which are simple open platforms (Fig. 1). Natural nest substrates included Granjeno, grass, Huisache (*Acacia smallii*), Lime Pricklyash, McCartney Rose, mesquite, unidentified tree, Yaupon, and yucca. Because falcons do not construct their own nests, we determined



FIG. 1. Two designs of artificial nests provided for Aplomado Falcons in southern Texas. The "platform" design on the left is an open platform mounted on a 6-m pole; the "barred" design on the right is a solid-topped box with conduit sides spaced to allow birds access to the nest, mounted on a 3.5-m pole.

TABLE 1. Aplomado Falcon nesting attempts by year and study area. "Successful nests" fledged at least one young.

	2002		2003		2004	
	LA ^a	MI ^b	LA	MI	LA	MI
Falcon pairs	17	9	21	11	20	11
Nest attempts	18	9	24	13	21	12
Successful nests	10	2	12	4	14	9

^aLaguna Atascosa NWR.^bMatagorda Island NWR.

the identity of the original nest-builder—Chihuahuan Ravens (*Corvus cryptoleucus*), Crested Caracaras (*Caracara cheriway*), White-tailed Hawks (*Buteo albicaudatus*), White-tailed Kites (*Elanus leucurus*), natural niches, or humans (artificial nests). We measured nest height from ground to rim of nest, estimated percentage of overhead cover concealing the nest in each cardinal direction (the mean of the four percentages was used for analysis), and mapped nest location with handheld global positioning system (GPS) units.

Modeling of daily nest-survival rate.—Because our sample size was insufficient to consider all levels of each categorical variable independently, we grouped nests into "types" guided by a cluster analysis considering only nest substrate and nest-builder. We coded the categorical variables as binary dummy variables and calculated a similarity matrix using Jaccard's coefficient of community (Legendre and Legendre 1998). We then performed a hierarchical agglomerative cluster analysis with Ward's minimum-variance linkage method to construct nest-type clusters. Cluster analyses were performed using the "hclust" and "vegan" packages for program R (see Acknowledgments).

Because we observed repeated nesting attempts by many of the same individuals across years, we examined the data for evidence of overdispersion that would indicate that the data were correlated, thus requiring analysis with generalized linear mixed models. We evaluated a logistic-exposure model of daily nest survival that contained all potential variables in R (Shaffer 2004). Because the dispersion parameter (ϕ) for this model, or the weighted sum of the squared Pearson residuals divided by model degrees of freedom, did not indicate that overdispersion was present in our data, we chose to model nest survival using MARK (Venables and Ripley 2002). We investigated DSR by constructing and evaluating models in MARK with nest types and study areas coded as separate groups (Dinsmore et al. 2002). We standardized the nest-initiation date to 1 for all nests but retained the true

nest-initiation date as a seasonal-effect covariate. This constrained our exposure period to the length of the nest cycle (67 days), allowing us to model effects of nest age as well as seasonality.

Using an information-theoretic approach, we evaluated a set of competing models investigating nest success by comparing Akaike's Information Criterion scores (AIC; Akaike 1973, Burnham and Anderson 2002). First, we identified the most appropriate nest-age trend by fitting models with all possible combinations of constant, linear, and quadratic time trends, either throughout the course of the nest cycle or stage-specific (i.e., age trend allowed to differ in incubation and nestling phases). Next, we examined nest-type and study-area effects and then iteratively added our nest-measurement and nest-initiation-date covariates. Finally, the best covariate plus time-trend model was investigated further by searching for stage-specific covariate effects.

RESULTS

We monitored 97 nesting attempts by 37 pairs (Table 1). Of these nests, 51 produced at least one fledgling, resulting in an overall apparent nest-survival rate of 53%. Apparent nest survival was higher at Laguna Atascosa NWR than at Matagorda Island NWR (57% vs. 44%).

Four nest-type groups emerged as distinct clusters with sample sizes sufficient for further analysis (Table 2). Cluster 1 was the most diverse group, containing mostly natural shrub and tree nests. The remaining groups were more well defined: cluster 2 included all nests placed in depressions on the ground, cluster 3 artificial platforms and birds' nests (only Chihuahuan Ravens' nests during present study) found on power transmission poles, and cluster 4 all remaining artificial nest structures (hereafter, "natural," "ground," "power-pole," and "artificial," respectively).

Nest age was important in modeling DSR. Quadratic and cubic nest-age trends fitted over the entire nest cycle were competitive, but DSR was best expressed as constant throughout the incubation phase, with the probability of nest survival increasing linearly throughout the nestling phase (Table 3). Nest-type groups were best modeled separately (sum of model weight, $\Sigma\omega_i = 0.999$), but additional consideration of study-site area was not well supported ($\Sigma\omega_i = 0.136$). Predicted nest success was 0% for ground nests, which is consistent with observed apparent nest survival and suggests that these sites were of low quality. Conversely, the highest success rates were predicted for artificial nests (predicted nest success = 86%; Fig. 2). Natural and power-pole nests exhibited similar DSR during incubation; however, power-pole nests survived at higher rates than natural

TABLE 2. Characteristics of Aplomado Falcon nest-type groups as identified by cluster analysis. Nest substrates and nest builders (original source of nest platform; either another bird, a naturally occurring "niche" depression, or artificial) are listed in order of contribution to cluster.

Cluster	n	Name	Nest substrates	Nest builders
1	53	Natural	Mesquite, Yaupon, yucca, McCartney Rose, Granjeno, tree, Lime Pricklyash, Huisache, power pole	Crested Caracara, White-tailed Hawk, White-tailed Kite, niche, Chihuahuan Raven, artificial
2	9	Ground	Grass	Niche
3	13	Power pole	Power pole	Chihuahuan Raven, artificial
4	22	Artificial	Platform, barred	Artificial

TABLE 3. Aplomado Falcon daily nest-survival rate (DSR) models that consider nest age only.

Nest age trend	AIC _c	ΔAIC _c	K ^a	Deviance
Incubation (.) ^b + Nestling (lin) ^c	300.192	0	3	294.186
Quadratic	300.630	0.438	3	294.624
Incubation (lin) + Nestling (lin)	303.078	2.886	3	297.072
Linear	304.338	4.146	2	300.335
Incubation (lin) + Nestling (lin)	304.920	4.728	3	298.914
Incubation (.) + Nestling (.)	306.867	6.675	3	300.861
Time ^d	407.315	107.123	67	271.054

^aNumber of model parameters.^bConstant DSR throughout nest phase.^cLinear trend in DSR during nest phase.^dDaily variation in DSR.

nests during the remainder of the nest cycle (predicted nest success of 40% vs. 71%; all model-averaged estimates).

Addition of the nest-height and overhead-cover covariates, but not nest initiation date, greatly improved the best age-trend model (Table 4). Because multiple models had similar model weights, we generated beta parameter estimates through model averaging (Table 5). Nest height positively influenced nest survival (overall $\Sigma\omega_i = 0.905$) but was more important during the nestling phase ($\Sigma\omega_i = 0.736$). Both overhead cover and its interaction with nest height were also positively correlated with DSR but were less important ($\Sigma\omega_i = 0.511$ and 0.259).

DISCUSSION

Nest age trend.—The present study—the first, to our knowledge, to model DSR in a raptor—was consistent with recent studies of passerines and shorebirds that found variation in DSR throughout the nest cycle (Jehle et al. 2004, Nur et al. 2004, Peak et al. 2004, Shaffer 2004, Lloyd and Martin 2005). As with other passerines, daily survival rates of falcon nests decreased during hatching and the early nestling phase, when parental and offspring behavior

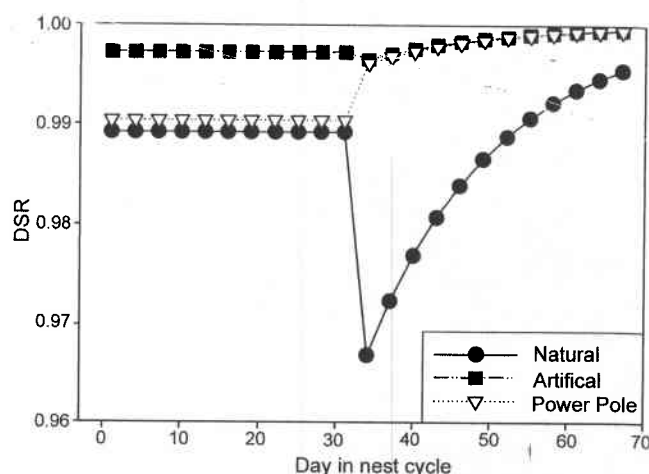


FIG. 2. Model-averaged predicted daily survival rates of Aplomado Falcon nests for natural, power-pole, and artificial nests in relation to day of the nesting cycle. Nest-type groups were assigned by cluster analysis.

changes abruptly (Grant et al. 2005). This change in behavior ostensibly provides additional cues to a wide variety of terrestrial (Coyote [*Canis latrans*]; Raccoon [*Procyon lotor*]) and avian predators (Great Horned Owl [*Bubo virginianus*]; Harris's Hawk [*Parabuteo unicinctus*]; Crested Caracara) that prey on eggs, nestlings, or unwary adults (Perez et al. 1996, Keddy-Hector 2000). We failed to detect any seasonal variability in DSR, unlike recent studies of shorebirds, waterfowl, and passerines (Dinsmore et al. 2002, Jehle et al. 2004, Nur et al. 2004, Shaffer 2004). Our modest sample size may prevent recognition of a seasonal trend; additionally, such trends may be moderated by the relative lack of seasonality in subtropical southern Texas.

Nest types and site covariates.—Nest survival was strongly related to nest type, which suggests that nest-type groupings represented additional variation not sufficiently represented by

TABLE 4. Top models ($\Delta AIC_c < 4.0$) describing Aplomado Falcon daily nest-survival rates (DSR), ranked by AIC_c scores. Basic age-trend model and model containing nest initiation-date term are included for comparison. All models feature an age-trend term of constant DSR during incubation and a linear trend during nestling phase

Covariates	Groups	K ^a	AIC _c	ΔAIC _c	w _i ^b	Deviance
NestHt ^c (nstl) ^d	Nest type	7	268.490	0	0.254	254.463
NestHt (nstl) + PerCov ^e + NestHt:PerCov ^f	Nest type	9	269.044	0.554	0.192	251.000
NestHt (nstl) + PerCov	Nest type	8	269.216	0.726	0.176	253.181
NestHt (nstl)	Study area, Nest type	8	270.095	1.605	0.114	254.060
NestHt + PerCov + NestHt:PerCov	Nest type	9	271.147	2.657	0.067	253.103
NestHt	Nest type	7	272.074	3.584	0.042	258.047
None	Nest type	6	273.543	5.053	0.020	261.523
Nest-initiation date	Nest type	7	275.457	6.967	0.008	261.430

^aNumber of model parameters.^bModel weight.^cNest height.^dDuring nestling phase only.^eOverhead cover.^fColon indicates an interaction between variables.

TABLE 5. Model-averaged beta parameter estimates and 95% confidence intervals (CI) for models of daily nest-survival rate in Aplomado Falcons.

Parameter	β	95% CI
Intercept	4.940	3.468 to 6.411
Incubation	0.821	-0.389 to 2.030
Nestling	0.061	0.001 to 0.122
Study area	0.031	-0.064 to 0.126
Natural nests	-1.214	-2.502 to 0.205
Ground nests	-2.753	-4.341 to -1.164
Power-pole nests	-1.160	-2.813 to 0.493
Nest height (entire nest cycle)	0.118	-0.011 to 0.246
Nest height (nestling phase only)	1.068	0.155 to 1.985
Overhead cover	0.180	-0.065 to 0.425
Nest height (overhead cover)	0.250	-0.048 to 0.547

physical nest-site covariates. Nest height was the most important physical site covariate, especially during the nestling phase (Fig. 3A). However, artificial nests outperformed natural nests of the same height, which again suggests inherent differences between nest types. Although there is some support for overhead cover affecting DSR, any effect was small once all competitive models were considered (Fig. 3B). This effect may be driven, in large part, by the difference in nest success between types of artificial nests; barred nests, which had 100% apparent nest success, are lower than platform nests but are completely covered.

Context of our results.—The DSR of falcons was highly variable yet well correlated with the nest-site characteristics of nest height and nest type. Either characteristic should be a reasonable indicator of nest-site quality and serve as a dependable cue for falcon nest-site selection. Yet falcons frequently (sometimes successively) used nest sites that should have been easily recognizable as poor-quality because of their proximity to the ground. Examination of nest-site selection in relation to nest-site availability by Aplomado Falcons should help determine whether the falcons choose nest sites to maximize annual productivity within the constraints of their territory, or whether trade-offs between current reproduction and the adults' residual reproductive value cause what appears to be maladaptive behavior. Conclusive links between nest-site selection and reproductive success in complex systems have yet to be firmly established (Misenhelter and Rotenberry 2000, Pöysä et al. 2001, Forstmeier and Weiss 2004). Considering falcons, one study of Peregrine Falcons (*F. peregrinus peregrinus*; hereafter "peregrines") in Spain found no relationship between habitat features and nest success (Gainzarain et al. 2000). A later study, however, found that Spanish peregrines appeared to select nest cliffs to maximize productivity, but the variables cited are landscape-level features also associated with high prey densities, thus potentially confounding nest-site selection with foraging (Sergio et al. 2004).

Behavioral traits may conflict with optimal nest-site selection. As with other falcons, breeding adults rely on platform-like structures provided by other birds' nests or those formed by vegetation or landform features, such as bowl-shaped depressions in epiphytic plant crowns (Cade 1982, Keddy-Hector 2000). Stick nests degrade rapidly, thus constituting an ephemeral resource

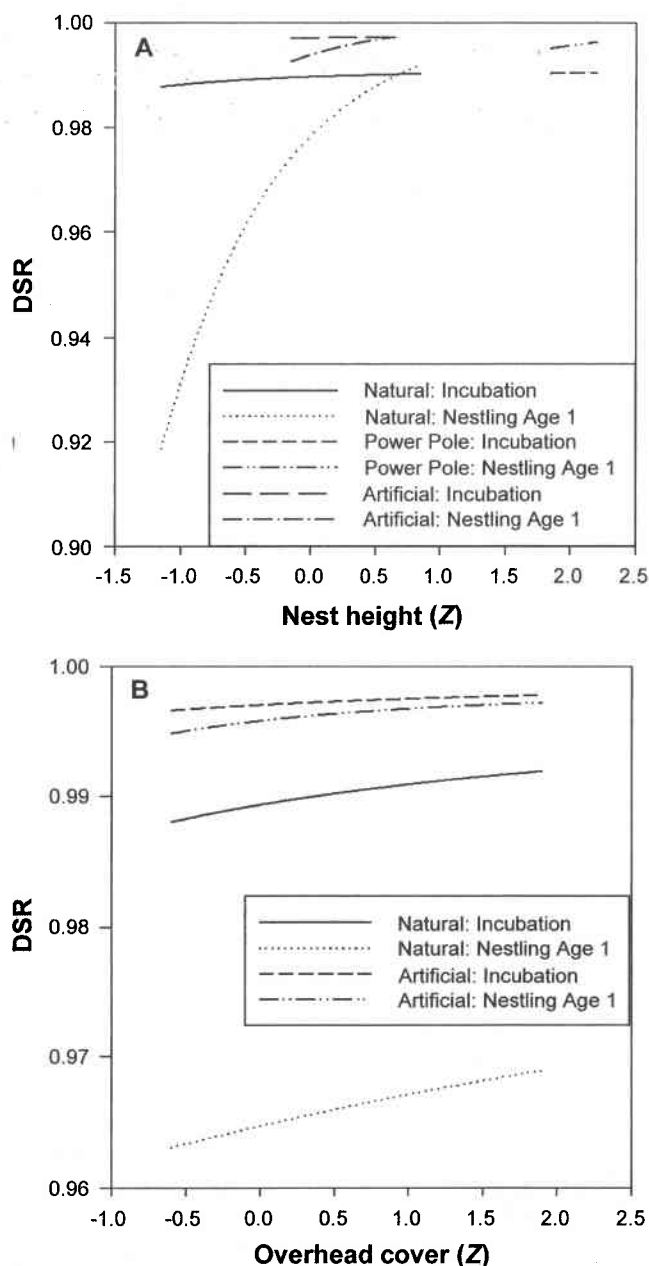


FIG. 3. Model-averaged daily nest-survival rates (DSR) during incubation and for day-old nestlings for natural, power-pole, and artificial nests, in relation to (A) nest height and (B) overhead cover.

different from the traditional cliff-side eyries preferred by other falcons (Keddy-Hector 2000, White et al. 2002). Accordingly, Aplomado Falcons must have the ability to recognize potential nest sites despite substantial geographic and temporal variation. The need to maintain broad criteria for identifying highly variable nest substrates may thus preclude selection of nest sites with an inherently high probability of success.

The tendency of Aplomado Falcons to switch nest sites frequently, possibly to avoid ectoparasitism or predation, further

complicates selection of nest sites (Keddy-Hector 2000, J. L. Brown and M. W. Collopy pers. obs). Bird nests used in consecutive years may become heavily infested by ectoparasites, potentially reducing survival of nestlings and adults (McFadzen and Marzluff 1996, Stanback and Rockwell 2003, Brown and Brown 2004). Long-lived birds risk experiencing additional cumulative costs from parasitic loads because decreased parental reproductive value resulting from the infestation is coupled with reduced reproductive value of the compromised young (Bize et al. 2004; Fitze et al. 2004a, b). Similarly, some mammalian predators will habitually revisit previously discovered nest sites, such that reuse of nest sites may increase the risk of predation (Hakkarainen et al. 2001). Therefore, shifting nest sites may result in underuse of rare, high-quality nest sites.

We also should consider the potential influence of nest-site imprinting; raptors form impressions about appropriate nest sites at an early age, which raises the possibility that captive-bred adults may have different nest-site evaluation criteria than wild-fledged birds (Fox 1995). Unlike their cliff-nesting counterparts, tree-nesting European peregrines have yet to recolonize their former range, which is attributable to the fact, recognized belatedly, that tree nesting is employed only by captive-bred peregrines that are imprinted on tree-nesting substrates (Kirmse 2001, Wegner et al. 2005).

We have no information regarding the relative availability of high- and low-quality nests within each territory and so cannot directly examine whether falcons were choosing the highest-quality nest sites possible. However, because all breeding adults could be classified as captive-bred or wild-fledged (all captive-bred and some wild falcons were marked; all marked breeding falcons were identified, and any unmarked breeding falcons were necessarily wild-fledged), we compared nest-site selection between falcons of differing origin. Generalized linear models considering a random effect of individual and a fixed effect of falcon origin showed no difference in nest heights between the two groups ($t = 0.967$, $df = 83$, $P = 0.336$). Therefore, inappropriate nest-site imprinting does not explain poor nest-site selection. We found little indication of

autocorrelation between attempts by the same individuals, which suggests that throughout the observation period, individual falcons chose a variety of nest heights (null model without autocorrelation, $AIC = 480.32$; null model with first-order autocorrelation for nesting attempt, $AIC = 479.77$).

Comparison of nesting success among falcons.—We cannot directly compare our estimate of nesting success in Northern Aplomado Falcons with those for other New World falcons, because published accounts for those species report apparent nesting success; yet patterns are suggested (Table 6). The Neotropical falcons, Aplomado Falcon, Bat Falcon (*F. ruficularis*), and Orange-breasted Falcon (*F. deiroleucus*), have similarly modest clutch sizes. These species not only share similar ranges but, purportedly, are close relatives, which complicates interpretation of patterns (Cade 1982, Keddy-Hector 2000). Nest-success rates of Orange-breasted and Aplomado falcons are comparable (mean overall success in our study = 51%); however, nest success reported for the cavity-nesting Bat Falcon was substantially higher. Considering only North American falcons, the Aplomado Falcon lays the fewest eggs per clutch and shares relatively low nest-success with the Gyrfalcon (*F. rusticolus*). The Merlin (*F. columbarius*) is the only other falcon that commonly uses stick nests in trees, yet estimates of clutch size and breeding productivity are higher than for the Aplomado Falcon.

Falcons that are ecologically convergent with the Aplomado Falcon inhabit arid lands in Africa and Australia, but few studies have reported reproductive parameters (Cade 1982). In a population of Red-necked Falcons (*F. chicquera*) in the African Kalahari, 8 of 19 nests fledged young (apparent success = 42%), and mean clutch size was 3.3 ± 0.5 eggs (Herholdt 1994). This species forages similarly to the Aplomado Falcon, in that pairs hunt small birds cooperatively in open country, but adults are markedly smaller (*F. chicquera*: female mass: 240 g, male mass: 160–180 g; *F. femoralis* in eastern Mexico: 9 females averaged 407 g, 7 males averaged 260 g; Osborne 1981, Cade 1982, Keddy-Hector 2000). Two larger falcons in Australia, the Brown Falcon (*F. berigora*: female mass ≈ 620 g) and Grey Falcon (*F. hypoleucus*: female mass ≈ 600 g)

TABLE 6. Reproductive parameters of New World falcons. Clutch sizes are means, unless otherwise indicated; sample sizes (n) are given in parentheses. Note that apparent nest success (number of successful nests divided by total number of nests found) is not equivalent to estimates of daily nest-survival rate (DSR).

Species	English name	Nest site	Clutch size	Apparent nest success	Sources
<i>Falco sparverius</i>	American Kestrel	Cavities	4.6 (^a)	0.65 (^a)	Smallwood and Bird 2002
<i>F. ruficularis</i>	Bat Falcon	Cavities (trees, cliffs, buildings)	2.9 (14)	0.86 (14)	Cade 1982
<i>F. columbarius</i>	Merlin	Stick nests (rarely cliff or ground)	4.2 ± 0.04 (163)	Not provided (^b)	Warkentin et al. 2005
<i>F. femoralis</i>	Aplomado Falcon	Stick nests	2.6 ± 0.8 (7)	0.43 (7)	Montoya et al. 1997
<i>F. deiroleucus</i>	Orange-breasted Falcon	Cliffs (trees, rarely buildings?)	2 to 3 (^a)	0.53 (59)	Cade 1982, Baker et al. 2000
<i>F. mexicanus</i>	Prairie Falcon	Cliffs, power poles	5 (mode; 1,206)	0.71 ± 0.18 (^a)	Steenhof 1998
<i>F. peregrinus</i>	Peregrine Falcon	Cliffs, buildings (rarely stick nests in trees)	3 to 4 (^a)	0.64 (2,301)	White et al. 2002
<i>F. rusticolus</i>	Gyrfalcon	Cliffs, ground (rarely stick nests in trees)	3.72 ± 0.71 (122)	0.52 (^a)	Clum and Cade 1994

^aSample size not provided.

^bProductivity per Merlin pair in North America ranged between 3.6 and 3.8 fledglings.

(Olsen and Marples 1993), occupy niches similar to the Aplomado Falcon's. Summaries of reproductive success are unavailable, but clutch sizes are comparable (*F. berigora*: mean clutch size = 2.8 ± 0.6 eggs; *F. hypoleucus*: mean clutch size = 2.6 ± 0.7 eggs; Olsen and Marples 1993). All three species primarily use stick nests constructed by other raptors or corvids. Thus, the relatively low productivity observed during our study may not be unusual among savannah-dwelling falcons.

ACKNOWLEDGMENTS

Aplomado Falcons are present in the United States thanks to The Peregrine Fund and its many dedicated workers, volunteers, and donors; special thanks to T. Cade, M. Curti, W. Burnham, E. Gott, W. Heinrich, J. Jenny, P. Juergens, B. and R. Mutch, A. Montoya, C. Sandfort, and countless hack site attendants who devoted so much time and effort to the recovery of this species. We thank G. Hunt, S. Jenkins, and J. Sedinger for their guidance. The manuscript was greatly improved by comments from J. Bart, M. Bechard, S. Sealy, and an anonymous reviewer. Research was supported in part by Nevada Agricultural Experiment Station, publication #52066955. This material is partially based on work supported by a National Science Foundation Graduate Research Fellowship (to J.L.B.). R statistical software is available at www.r-project.org/.

LITERATURE CITED

- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in *Second International Symposium on Information Theory* (B. N. Petrov and F. Csáki, Eds.). Akadémiai Kiadó, Budapest, Hungary.
- BAKER, A. J., D. F. WHITACRE, O. A. AGUIRRE-BARRERA, AND C. M. WHITE. 2000. The Orange-breasted Falcon *Falco deiroleucus* in Mesoamerica: A vulnerable, disjunct population? *Bird Conservation International* 10:29–40.
- BIZE, P., A. ROULIN, J. L. TELLA, L.-F. BERSIER, AND H. RICHNER. 2004. Additive effects of ectoparasites over reproductive attempts in the long-lived Alpine Swift. *Journal of Animal Ecology* 73:1080–1088.
- BROWN, C. R., AND M. B. BROWN. 2004. Group size and ectoparasitism affect daily survival probability in a colonial bird. *Behavioral Ecology and Sociobiology* 56:498–511.
- BROWN, J. L., M. W. COLLOPY, E. J. GOTT, P. W. JUERGENS, A. B. MONTOYA, AND W. G. HUNT. 2006. Wild-reared Aplomado Falcons survive and recruit at higher rates than hacked falcons in a common environment. *Biological Conservation* 131:453–458.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*, 2nd ed. Springer-Verlag, New York.
- CADE, T. J. 1982. *The Falcons of the World*. Cornell University Press, Ithaca, New York.
- CLUM, N. J., AND T. J. CADE. 1994. Gyrfalcon (*Falco rusticolus*). In *The Birds of North America*, no. 114 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- DINSMORE, S. J., G. C. WHITE, AND F. L. KNOPE. 2002. Advanced techniques for modeling avian nest survival. *Ecology* 83:3476–3488.
- FITZE, P. S., J. CLOBERT, AND H. RICHNER. 2004a. Long-term life-history consequences of ectoparasite-modulated growth and development. *Ecology* 85:2018–2026.
- FITZE, P. S., B. TSCHIRREN, AND H. RICHNER. 2004b. Life history and fitness consequences of ectoparasites. *Journal of Animal Ecology* 73:216–226.
- FORSTMEIER, W., AND I. WEISS. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* 104:487–499.
- FOX, N. 1995. *Understanding the Bird of Prey*. Hancock House, Blaine, Washington.
- GAINZARAIN, J. A., R. ARAMBARRI, AND A. F. RODRÍGUEZ. 2000. Breeding density, habitat selection and reproductive rates of the Peregrine Falcon *Falco peregrinus* in Álava (northern Spain). *Bird Study* 47:225–231.
- GRANT, T. A., T. L. SHAFFER, E. M. MADDEN, AND P. J. PIETZ. 2005. Time-specific variation in passerine nest survival: New insights into old questions. *Auk* 122:661–672.
- HAKKARAINEN, H., P. ILMONEN, V. KOIVUNEN, AND E. KORPIMÄKI. 2001. Experimental increase of predation risk induces breeding dispersal of Tengmalm's Owl. *Oecologia* 126:355–359.
- HEPPELL, S. S., H. CASWELL, AND L. B. CROWDER. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. *Ecology* 81:654–665.
- HERHOLDT, J. J. 1994. Aspects of the breeding ecology of the Red-necked Falcon *Falco chicquera horsbrughii* and its hunting association with the Gabar Goshawk *Micronisus gabar* in the south-eastern Kalahari. Pages 123–132 in *Raptor Conservation Today* (B.-U. Meyburg and R. D. Chancellor, Eds.). World Working Group on Birds of Prey and Pica Press, London.
- JAHRSDOERFER, S. E., AND D. M. LESLIE, JR. 1988. Tamaulipan brushland of the Lower Rio Grande Valley of south Texas: Description, human impacts, and management options. U.S. Department of Interior, Fish and Wildlife Service, Biological Report no. 88.
- JEHLE, G., A. A. YACKEL ADAMS, J. A. SAVIDGE, AND S. K. SKAGEN. 2004. Nest survival estimation: A review of alternatives to the Mayfield estimator. *Condor* 106:472–484.
- JENNY, J. P., W. HEINRICH, A. B. MONTOYA, B. MUTCH, C. SANDFORT, AND W. G. HUNT. 2004. From the field: Progress in restoring the Aplomado Falcon to southern Texas. *Wildlife Society Bulletin* 32:276–285.
- KEDDY-HECTOR, D. P. 2000. Aplomado Falcon (*Falco femoralis*). In *The Birds of North America*, no. 549 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- KIRMSE, V. W. 2001. Reintroduction of tree-nesting peregrines (*Falco peregrinus*) in central Europe. *Zeitschrift für Jagdwissenschaft* 47:165–177.
- LEGENDRE, P., AND L. LEGENDRE. 1998. *Numerical Ecology*, 2nd ed. Elsevier, Amsterdam, The Netherlands.
- LLOYD, J. D., AND T. E. MARTIN. 2005. Reproductive success of Chestnut-Collared Longspurs in native and exotic grassland. *Condor* 107:363–374.

- MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- MCALISTER, W. H., AND M. K. MCALISTER. 1993. Matagorda Island: A Naturalist's Guide. University of Texas Press, Austin.
- McFADZEN, M. E., AND J. M. MARZLUFF. 1996. Mortality of Prairie Falcons during the fledging-dependence period. *Condor* 98:791–800.
- MISENHELTER, M. D., AND J. T. ROTENBERRY. 2000. Choices and consequences of habitat occupancy and nest site selection in Sage Sparrows. *Ecology* 81:2892–2901.
- MONTÓYA, A. B., P. J. ZWANK, AND M. CARDENAS. 1997. Breeding biology of Aplomado Falcons in desert grasslands of Chihuahua, Mexico. *Journal of Field Ornithology* 68:135–143.
- NUR, N., A. L. HOLMES, AND G. R. GEUPEL. 2004. Use of survival time analysis to analyze nesting success in birds: An example using Loggerhead Shrikes. *Condor* 106:457–471.
- OLSEN, P. D., AND T. G. MARPLES. 1993. Geographic variation in egg size, clutch size and date of laying of Australian raptors (Falconiformes and Strigiformes). *Emu* 93:167–179.
- OSBORNE, T. O. 1981. Ecology of the Red-necked Falcon *Falco chicquera* in Zambia. *Ibis* 123:289–297.
- PEAK, R. G., F. R. THOMPSON III, AND T. L. SHAFFER. 2004. Factors affecting songbird nest survival in riparian forests in a midwestern agricultural landscape. *Auk* 121:726–737.
- PEREZ, C. J., P. J. ZWANK, AND D. W. SMITH. 1996. Survival, movements and habitat use of Aplomado Falcons released in southern Texas. *Journal of Raptor Research* 30:175–182.
- PÖYSÄ, H., V. RUUSILA, M. MILONOFF, AND J. VIRTANEN. 2001. Ability to assess nest predation risk in secondary hole-nesting birds: An experimental study. *Oecologia* 126:201–207.
- RICKLEFS, R. E. 2000. Density dependence, evolutionary optimization, and the diversification of avian life histories. *Condor* 102:9–22.
- RICKLEFS, R. E., AND M. WIKELSKI. 2002. The physiology/life-history nexus. *Trends in Ecology and Evolution* 17:462–468.
- ROFF, D. A. 2002. Life History Evolution. Sinauer Associates, Sunderland, Massachusetts.
- SÆTHER, B.-E., AND Ø. BAKKE. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81:642–653.
- SERGIO, F., F. RIOZZOLLI, L. MARCHESI, AND P. PEDRINI. 2004. The importance of interspecific interactions for breeding-site selection: Peregrine Falcons seek proximity to raven nests. *Ecography* 27:818–826.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- SMALLWOOD, J. A., AND D. M. BIRD. 2002. American Kestrel (*Falco sparverius*). In *The Birds of North America*, no. 602 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- STANBACK, M. T., AND E. K. ROCKWELL. 2003. Nest-site fidelity in Eastern Bluebirds (*Sialia sialis*) depends on the quality of alternate cavities. *Auk* 120:1029–1032.
- STEENHOF, K. 1998. Prairie Falcon (*Falco mexicanus*). In *The Birds of North America*, no. 346 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- VENABLES, W. N. AND B. D. RIPLEY. 2002. Modern Applied Statistics with S, 4th ed. Springer-Verlag, New York.
- WARKENTIN, I. G., N. S. SODHI, R. H. M. ESPIE, A. F. POOLE, L. W. OLIPHANT, AND P. C. JAMES. 2005. Merlin (*Falco columbarius*). *The Birds of North America Online* (A. Poole, Ed.). Cornell Laboratory of Ornithology, Ithaca, New York. Available at bna.birds.cornell.edu/BNA/account/Merlin/.
- WEGNER, P., G. KLEINSTÄUBER, F. BAUM, AND F. SCHILLING. 2005. Long-term investigation of the degree of exposure of German Peregrine Falcons (*Falco peregrinus*) to damaging chemicals from the environment. *Journal of Ornithology* 146:34–54.
- WHITE, C. M., N. J. CLUM, T. J. CADE, AND W. G. HUNT. 2002. Peregrine Falcon (*Falco peregrinus*). In *The Birds of North America*, no. 660 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.

Associate Editor: M. Bechard