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TEMPORAL INSTABILITY OF AGRICULTURAL HABITAT REDUCES REPRODUCTIVE SUCCESS OF BARN OWLS (*TYTO ALBA*)

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Abstract.—Birds are generally unable to predict future changes in habitat condition when selecting nesting locations, and few studies have investigated the effect on birds of shifting habitat quality within nesting seasons. Anthropogenically influenced habitats such as agricultural landscapes are often associated with large shifts in quality that turn initially good habitat into poor habitat. We examined whether daily survival rates of Barn Owl (*Tyto alba*) nests in an agricultural landscape were influenced negatively by temporal instability in habitat conditions resulting from crop harvest. Although most nesting attempts by Barn Owls in our study area were initiated before the onset of harvest, fields adjacent to the majority of active nest boxes were harvested at some point during nesting attempts. Overall nest survivorship, as well as survivorship of individual nestlings within broods, was lower following harvest, likely because of associated declines in the abundance of rodents, the primary food source of Barn Owls. Nestlings in nests surrounded by harvested fields were generally lighter before fledging than young in nests surrounded by standing sugarcane and their associated dense rodent populations. Although instability of habitat quality in our study area was associated with reduced survivorship of individual Barn Owl nests, a population-level effect is unlikely given the overall fecundity of the population. *Received 22 October 2009, accepted 4 May 2010.*

Key words: agriculture, Barn Owl, ecological trap, habitat quality, nesting success, temporal instability, *Tyto alba*.

La Inestabilidad Temporal de un Hábitat Agrícola Reduce el Éxito Reproductivo de *Tyto alba*

Resumen.—Generalmente, las aves son incapaces de predecir los cambios futuros en las condiciones del hábitat cuando seleccionan sus sitios de anidación. Además, pocos estudios han investigado el efecto que tienen los cambios en la calidad del hábitat de anidación a lo largo de una temporada reproductiva sobre las aves. Los hábitas con influencia humana, como los paisajes agrícolas, frecuentemente se asocian con cambios marcados en la calidad que implican que hábitats inicialmente buenos pueden volverse pobres. Evaluamos si las tasas diarias de supervivencia de los nidos de *Tyto alba* en un paisaje agrícola se vieron afectadas negativamente por la inestabilidad temporal en las condiciones del hábitat causada por la cosecha. Aunque la mayoría de los intentos de anidación por parte de *T. alba* en nuestra área de estudio fueron iniciados antes del comienzo de la cosecha, los campos adyacentes a la mayoría de las cajas de anidación activas fueron cosechados en algún momento durante la anidación. La supervivencia general de los nidos y la supervivencia de los pichones dentro de las camadas fueron menores después de la cosecha, probablemente debido a las disminuciones asociadas en la abundancia de los roedores, que son la principal fuente de alimento para *T. alba*. Los pichones de nidos rodeados por campos cosechados fueron generalmente más livianos antes de abandonar el nido que los pichones de nidos rodeados por caña de azúcar, con sus poblaciones densas de roedores asociadas. Aunque la inestabilidad de la calidad del hábitat en nuestra área de estudio se asoció con una supervivencia reducida de los nidos individuales de *T. alba*, un efecto a nivel de la población resulta poco probable debido a su fecundidad general.

Avian species select breeding habitat and nesting locations by assessing habitat quality using environmental cues (Petit and Petit 1996, Muller et al. 1997, Martin 1998, Kolbe and Janzen 2002). Anthropogenic changes to habitat may cause these cues to become inaccurate as a gauge of habitat suitability (Misenhelter and Rotenberry 2000, Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006). An integral component of habitat suitability is the temporal stability of habitat conditions (Orians and Wittenberger 1991). Organisms must predict long-term suitability of habitat on the basis of an immediate assessment of quality and do not have the ability to reject good habitat that will be altered at some point in the future.

Temporal instability of habitat quality may be especially consequential when organisms select breeding sites (Orians and Wittenberger 1991). A bird may recognize that a chosen nest location is undesirable following the onset of nesting, but it may be unable to relocate because of physiological or behavioral limitations, or simply because not enough time remains in the breeding season

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to complete a nesting cycle at a new location. Therefore, temporal changes in habitat conditions, specifically the deterioration of nesting locations during the breeding season, may result in decreased reproductive success of individuals, with the outcome that the area functions as an ecological trap (Easton and Martin 1998, Beyeler 2009; but see Burhans and Thompson 1998). For example, grassland birds often establish nests in croplands because the structure of these systems mimics that of natural grasslands and, thus, they are perceived as good-quality habitat. However, structural changes to agricultural habitat that occur following the onset of nesting (e.g., crop growth, tillage, and harvest) can result in nest failure (Best 1986, Galbraith 1989, Bollinger et al. 1990).

Although several studies have investigated the influence of temporal instability of habitat conditions on songbird nest success (e.g., Burhans and Thompson 1998, Easton and Martin 1998, Beyeler 2009), few have investigated the influence of variation in habitat quality within breeding seasons on the reproductive success of raptors. Interyear variation in the productivity of Barn Owls (*Tyto alba*) has been linked to multiyear fluctuations in prey abundance (Taylor 1994, Marti 1998), but the influence of changes in habitat quality within breeding seasons on the daily survival of nests has not been demonstrated for this species. Our objective was to determine whether daily survival rates of Barn Owl nests associated with an agricultural landscape are influenced negatively by temporal instability in habitat conditions that result from crop harvest patterns. We specifically investigated whether declines in rodent populations caused by sugarcane harvest resulted in daily nest survival rates of Barn Owls that were significantly different than those of nests in which all nestlings fledged before the onset of harvest.

METHODS

Study location.—The Everglades Agricultural Area (EAA) is an approximately 160,000-ha region in southern Florida (Fig. 1) in which sugarcane is the primary crop. Individual sugarcane fields are harvested from November through March, following a 10- to 14-month growing season. Harvest occurs in a patchwork manner, with only a few adjacent fields harvested simultaneously. As harvest progresses, the EAA landscape becomes an increasingly sparse mosaic of standing sugarcane. Rodents, particularly Hispid Cotton Rats (*Sigmodon hispidus*; hereafter "cotton rats"), Black Rats (*Rattus rattus*; hereafter "roof rats"), and Marsh Rice Rats (*Oryzomys palustris*; hereafter "rice rats"), are abundant in sugarcane fields during most of the year but do not remain in fields after harvest (Holler et al. 1981, Lefebvre et al. 1989, Martin et al. 2007). Thus, an intra-annual population cycle exists that is driven by the cropping cycle (Martin 2009).

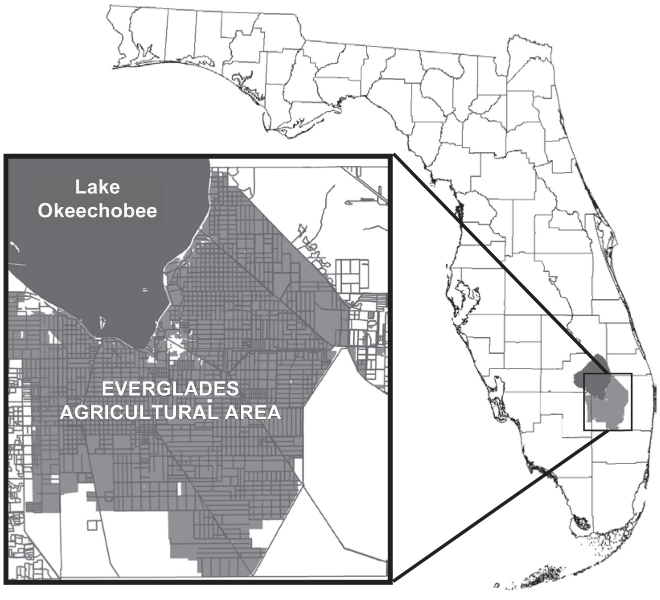

FIG. 1. Location of the Everglades Agricultural Area in Florida.

Study species.—Barn Owls occur in grasslands, agricultural fields, and other open habitat throughout most of the world and are declining throughout much of North America (Marti 1992, Taylor 1994). Historically, abundance of Barn Owls in the EAA has been limited because trees large enough to contain hollow spaces and buildings suitable for nesting and roosting are not common. Approximately 200 nest boxes have been installed throughout the EAA to enhance the local Barn Owl population. At least two-thirds of these boxes are occupied during any given nesting season (late August through early July; Martin 2009). Consequently, Barn Owl density is generally much greater in the EAA than in other landscapes, reaching a maximum of ~18 pairs 5 km^{-2} (Martin 2009). Densities elsewhere range from 0.7 pairs 5 km^{-2} to 2.6 pairs 5 km^{-2} (Taylor et al. 1988, Altwegg et al. 2003). When Barn Owls initiate reproduction, most crop fields in the EAA contain mature sugarcane. Given the relatively long nesting chronology of this species (~90 days; Marti 1992, Taylor 1994) and its ability to double-brood, many nestling Barn Owls in the EAA are exposed to declines in food availability as sugarcane fields adjacent to active nest boxes are harvested.

Estimating rodent abundance.—To confirm that rodent abundance in the EAA is linked to the sugarcane cropping cycle, we estimated the abundance of cotton rats, roof rats, and rice rats three times during each of two successive sugarcane growing seasons along the edges of 24 fields located throughout the EAA. Surveys were restricted to field edges because the interiors of sugarcane fields were inaccessible for much of the year because of the growth pattern of sugarcane plants. The resulting abundance estimates served as relative indices for comparing variation in rodent abundance over time. Initial surveys were conducted from mid-January through mid-March 2005 along the edges of 12 recently harvested fields. Second surveys took place in the same locations midway through the growing season (mid-May through mid-July). We conducted final surveys immediately prior to harvest (mid-September through mid-December). Rodents were surveyed in 2006, following the same time frame, along edges of 12 new fields. New survey sites were selected because several fields that were surveyed in 2005 were taken out of production or rotated to other crops.

We established two parallel transects interior to the outermost crop rows at each survey site. Transects were 250 m in length and separated by ~20 m. Two live traps (40.5 × 12.5 × 12.5 cm; Tomahawk Live Trap Company, Tomahawk, Wisconsin) were placed every 10 m along each transect (100 traps per survey site). For five consecutive days, we baited traps with rolled oats, opened them between 1600 and 1800 hours, then checked and closed them the following morning between 0700 and 1000 hours. We uniquely marked all captured cotton, roof, and rice rats by clipping their fur and recorded the species, sex, and mass of each. Immediately after processing, we released the rats at the capture location. Fur clips were not retained beyond each 5-day trapping session.

Barn Owl dietary analysis.—Barn Owls typically swallow prey whole and later regurgitate compacted pellets of indigestible bones and fur (Taylor 1994). Examination of prey remains found in these pellets is a reliable indicator of diet (Errington 1932, Raczynski and Ruprecht 1974, Dobson and Wexlar 1979). To determine whether cotton rats, roof rats, and rice rats constitute a significant portion of the Barn Owl diet in the EAA, we examined the contents of 1,676 pellets collected between May 2004 and February 2007 from throughout the area. Small mammal skulls from pellets were identified to species using reference specimens provided by the Florida Museum of Natural History. Rabbits were identified to genus (*Sylvilagus*), frogs and toads were identified to order (Anura), and birds were identified to class (Aves). The total number of skulls belonging to each species or taxonomic group was counted, and the relative percentage of each was calculated to determine the proportion in the diet of EAA Barn Owls.

Monitoring overall nest success.—We monitored 93 Barn Owl nesting attempts in nest boxes in the EAA from 1 December 2004 through 31 January 2007, over 801 nest-check intervals and 7,231 exposure days. Most nests that were initiated before 1 November during the 2005–2006 nesting season were destroyed by Hurricane Wilma; therefore, only nests initiated after that date were included from that year. Box contents were inspected visually or by using a video camera system mounted on the end of an extendable pole approximately every 7 days. If one egg was present after a check with no eggs, the nest box was not checked for 2 weeks to minimize the risk of abandonment. Following this, we visited occupied boxes weekly until broods either fledged or failed and counted the number of eggs and nestlings present during each visit. Nesting attempts were considered successful if at least one nestling survived to the expected fledging date for the nest, which was calculated as 60 days from the hatching date of the middle chick. Our monitoring efforts often enabled us to establish nest age to within 7 days because the first egg frequently appeared between 2 days when we checked boxes. If more than one egg was present when an occupied box was discovered, we determined the approximate nest age by multiplying 2.5 days (average interval between the laying of successive eggs in Barn Owls; Taylor 1994) by the number of eggs present before the appearance of a new egg. When nestlings were present, nest age was determined by multiplying 2.5 days by the number of nestlings and adding 30 days (average incubation period for the species; Taylor 1994). Occupied boxes were always located before all eggs hatched. Mean temperature and total rainfall for each check interval were obtained from the Florida Automated Weather Network station at the Everglades Research and Education Center, Belle Glade, Florida.

Habitat assessment.—We assessed habitat surrounding occupied nest boxes to examine the influence of sugarcane harvest on nest survivorship. We plotted the coordinates of all nest boxes onto a map of the EAA agricultural fields using ARCMAP, version 9.2 (ESRI, Redlands, California). Crop type (sugarcane, rotational, or fallow) and harvest date of individual sugarcane fields were obtained from landowners. We then created individual field maps for each year of the study that described land-cover and harvesting chronology. Only fields with standing sugarcane were considered suitable sources of prey for Barn Owls. Rotational crops (e.g., sod, rice, sweet corn, and leafy vegetables) and fallow fields were unlikely to harbor significant rodent populations because of lack of cover, the presence of standing water, a short growing season with frequent soil disturbance, frequent application of rodenticides, or a combination of these factors. We determined whether at least one standing sugarcane field occurred within an approximated home range of Barn Owls (706 ha; Marti 1992) around each box on each check date.

Vehicle strikes may be a significant source of mortality for Barn Owls in the EAA (J. M. Martin pers. obs.). Therefore, we also determined whether at least one major road occurred within 1,500 m of each nest box using the 2000 TIGER/Line file for Florida roads (U.S. Census Bureau). Roads described in the data set as "primary" or "secondary," as well as those frequently used to get to sugarcane mills, were considered major roads.

Monitoring within-nest survivorship.—To examine the relationship between sugarcane harvest and within-nest patterns of survivorship, we monitored the fates of 84 nestling Barn Owls in a subset of 18 nests. Eleven "postharvest" nests were monitored from 7 January to 23 May 2006 in areas where all sugarcane fields within 1,500 m of each nest box were harvested before nest initiation. This distance represents the approximate size of a Barn Owl home range (Hegdal and Blaskiewicz 1984, Marti 1992, Taylor 1994). Seven "preharvest" nests were monitored from 30 August to 22 December 2006 in areas where harvesting activities in fields within 1,500 m did not commence until after all nestlings had fledged. The cropping cycle follows a seasonal pattern, so the effects of harvest and season on survivorship of nests cannot be examined separately. All nests were monitored following the previously described protocol; however, they were visited more frequently around the estimated hatching date (30 days from lay date; Marti 1992) to mark individual nestlings. Colored nail polish was applied to the talons of newly hatched nestlings to facilitate identification of individuals. Once tarsi were fully developed (~30 days from hatching), uniquely numbered U.S. Fish and Wildlife Service lock-on leg bands were applied. After all nestlings within a brood were marked, we checked nest boxes weekly until they failed or fledged. During each visit, we recorded age, mass, tarsus length (tibio-tarsal articulation to palm), and wing chord (wrist to tip of unflattened, closed wing) for each nestling.

Statistical analysis.—We estimated the abundance of cotton rats, roof rats, and rice rats at each survey site using Huggins closed-capture modeling in program MARK (White and Burnham 1999). We modeled species-specific capture and recapture probabilities and incorporated heterogeneity in detection probability of individual rodents using sex and age as covariates (Martin 2009). The rodent populations were assumed to be closed during each 5-night trapping period. To examine the influence of the sugarcane cropping cycle on the abundance of each species of rodent, we analyzed final abundance estimates for each using a repeated-measures analysis of variance with sugarcane growth period (early, middle, late), year, and period*year as covariates (Martin 2009; Proc Mixed in SAS, version 9.1; SAS Institute, Cary, North Carolina). Appropriate covariance structures were selected using best-fit statistics, and a significance level of $P = 0.05$ was used throughout.

We used the logistic-exposure method (Shaffer 2004) in Proc Genmod (SAS) to model the influence of various predictor variables on the daily survival rate of 93 Barn Owl nests. Prior to analysis, we developed the following set of candidate explanatory models: (1) date (ordinal date of check); (2) nest_age (age of nest); (3) nest_year; (4) temperature and rain; (5) phase (incubation or brood rearing); (6) sugarcane (presence–absence of standing sugarcane within 1,500 m of nest); (7) road (presence–absence of a major road within 1,500 m of nest); (8) sugarcane and road; (9) sugarcane and phase; (10) phase and road; and (11) sugarcane, phase, and road.

For the subset of nests in which the fate of individual nestlings was monitored, we modeled daily survival rate for each nestling during the brood-rearing phase only by fitting logistic exposure models using Proc NLmixed in SAS. Daily survival rates of nestlings within broods are not independent from each other because all are exposed to nest-wide stressors (e.g., poor parental condition). Therefore, nest was included as a random variable in all models. We developed the following *a priori* predictive model set: (1) order (order that nestling hatched within brood); (2) age (age of nestling); (3) harvest (pre- or postharvest); (4) age and harvest; (5) order and harvest; (6) order and age; (7) age, order, and harvest; (8) harvest*age; (9) order*age; (10) harvest and order*age; and (11) order and harvest*age. We were unable to include the interaction of harvest and order in the model set because of insufficient data. Number of siblings was not included in the analysis because all brood sizes were similar ($\bar{x} = 4.9 \pm 0.2$ [SE]).

We verified the fit of the most parameterized model for each data set using the Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 2000) and used Akaike's information criterion (Burnham and Anderson 2002) to rank competing models. Best models were selected by judging degree of support as measured by ΔAIC_c and Akaike weights. Models with $\Delta AIC_c \le 2$ were considered competitive. To account for uncertainty in model selection, we also calculated model-averaged weighted parameter estimates and their associated standard errors and 95% confidence intervals (CIs) (Burnham and Anderson 2002, Shaffer 2004). We then used these values to calculate odds ratios and their associated 95% CIs. Odds ratios provide a direct interpretation of the influence of a variable on nest success (e.g., Peak et al. 2004, Lloyd and Martin 2005). Odds ratio values >1 indicate a positive effect, and those <1 indicate a negative effect. If the 95% CI of the odds ratio encompasses 1, no significant effect is indicated. We estimated daily survival rates for each level of explanatory variables that had significant odds ratios using the range of observed values of the covariates while holding all other covariates in the models constant (Shaffer and Thompson 2007).

To examine the influence of sugarcane harvest on the morphological development of nestlings, we first divided the nestlings into four groups: preharvest survived ($n = 23$), preharvest died ($n = 5$), postharvest survived ($n = 28$), and postharvest died ($n = 28$). Because the sample size of preharvest nestlings that died before fledging was small, we eliminated this group from the analysis. We then used a repeated-measures approach in Proc Mixed (SAS), with nest and age as random variables, to compare mass, tarsus length, and wing chord among the three remaining groups. Appropriate covariance structures were selected using best-fit statistics. Data from the two groups that survived to fledge were truncated to the maximum observed age of postharvest nestlings that died (54 days) to facilitate comparisons among groups. We used Bonferroni adjusted *P* values to perform pairwise comparisons among groups. This multiple-comparison correction is a more conservative approach than using standard *P* values (Wright 1992).

TABLE 1. Results of a repeated-measures analysis of variance examining the effects of sugarcane growth period and year on abundance estimates of cotton rats, roof rats, and rice rats in the Everglades Agricultural Area, 2005–2006.

		Cotton rats		Roof rats		Rice rats	
Effect	df	*F*	*P*	*F*	*P*	*F*	*P*
Sugarcane growth period	2	45.33	<0.01	12.06	<0.01	9.61	<0.01
Year	1	0.00	0.97	4.42	0.06	1.75	0.20
Growth period*year	2	0.56	0.58	1.66	0.21	0.90	0.42

RESULTS

Estimating rodent abundance.—Sugarcane growth period was a highly significant factor in determining the abundance of cotton rats, roof rats, and rice rats (Table 1). Low abundances were observed for all species following harvest, and abundances increased as the sugarcane growth cycle progressed (Fig. 2). Year was not a significant factor for any species; nor was the interaction of growth period and year (Table 1).

Barn Owl diet analysis.—Cotton rats (42%), roof rats (10%), and rice rats (8%) constituted 60% of the 2,146 prey items found in the owl pellets. House Mice (*Mus musculus*) also accounted for a relatively large portion of the Barn Owl diet (29%). The remainder consisted of rabbits (5%), birds (4%), Round-tailed Muskrats (*Neofiber alleni*; 1%), Southeastern Shrews (*Sorex longirostris*; 0.7%), and anurans (0.3%). Insect remains were found in many pellets but were not quantified.

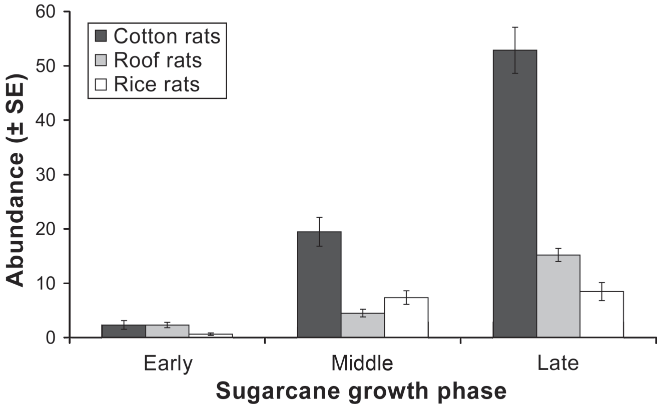

FIG. 2. Mean abundance indices of cotton rats, roof rats, and rice rats sampled in the early, middle, and late phases of the sugarcane cropping cycle in the Everglades Agricultural Area.

TABLE 2. Model fit for analysis of daily survival rate of 93 Barn Owl nests in the Everglades Agricultural Area, 2004–2007 (K is the number of model parameters, AIC_c is Akaike's information criterion with a second-order correction for small sample size, ΔAIC_c is the difference between a particular model and the top ranked model, and w_i is the model weight).

Model	K	AIC_c	ΔAIC_c	w_i
Sugarcane + phase	3	127.07	0.00	0.503
Sugarcane + road	3	127.20	0.12	0.472
Temperature + rain	3	133.23	6.15	0.023
Road	2	139.31	12.24	0.001
Constant	1	141.36	14.29	0.001
Sugarcane + phase + road	4	179.13	52.06	0.000
Phase + road	3	186.34	59.26	0.000
Sugarcane	2	186.44	59.37	0.000
Date	2	191.90	64.83	0.000
Phase	2	192.01	64.94	0.000
Nest_age	2	198.10	71.03	0.000
Nest_year	2	202.06	74.98	0.000

Daily nest survival.—Seventy-one of the 93 nesting attempts monitored (76%) were successful. Eighty-two nesting attempts (88%) were in nest boxes surrounded primarily by unharvested sugarcane fields at the time of nest initiation. Of these, sugarcane was removed entirely within 1,500 m of 53 nests and was partially removed within 1,500 m of an additional 29 nests at some point during nesting. Eleven of the 93 nests (12%) were established in nest boxes after all sugarcane fields within 1,500 m had been harvested. At least one major road occurred within 1,500 m of 58 nests (62%).

TABLE 3. Model-averaged parameter estimates (± SE) and odds ratio values of predictor variables of Barn Owl daily nest success in the Everglades Agricultural Area, 2004–2007.

Variable	Model-averaged parameter estimate	Odds ratio	95% CI
Sugarcane (present vs. absent)	2.14 ± 0.82	8.50	1.67–43.38
Phase (incubation vs. brood rearing)	0.78 ± 1.04	2.18	0.27–17.46
Road (absent vs. present)	0.56 ± 0.76	1.75	0.38–8.08
Rain	0.01 ± 0.02	0.99	0.94–1.03
Temperature	0.00 ± 0.01	0.99	0.98–1.01
Date	0.00 ± 0.00	1.00	1.00–1.00
Nest_age	0.00 ± 0.00	1.00	1.00–1.00
Nest_year (spring 2006 vs. spring 2005)	0.00 ± 0.00	1.00	1.00–1.00
Nest_year (fall 2006 vs. spring 2005)	0.00 ± 0.00	1.00	1.00–1.00

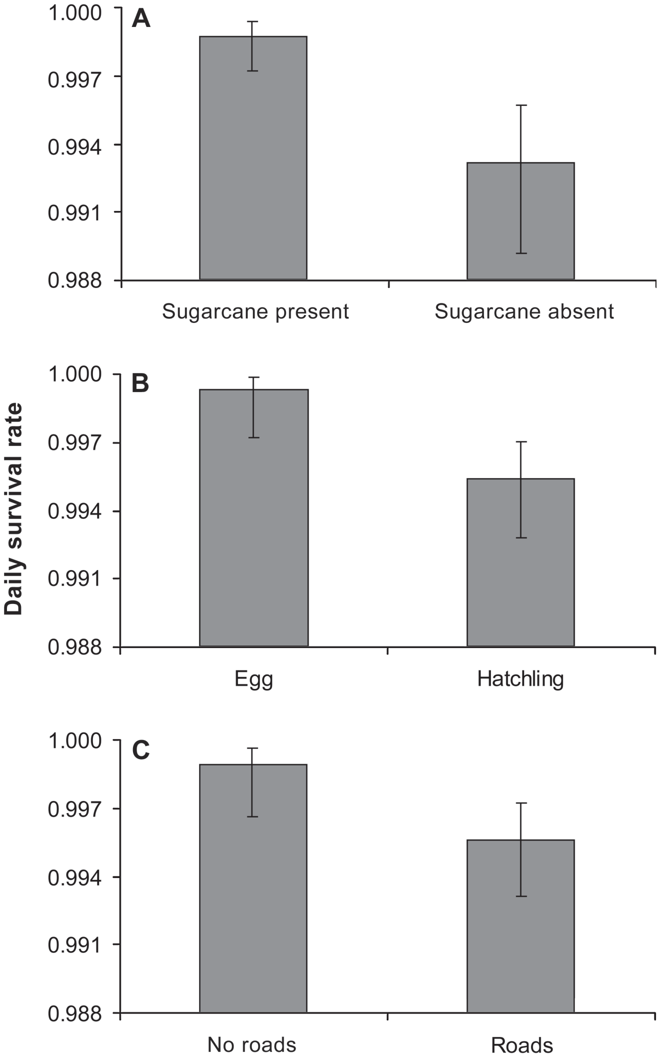

FIG. 3. Daily survival rates (± 95% CI) for Barn Owl nests in the Everglades Agricultural Area (2004–2006) (A) when sugarcane was present or absent within 1,500 m, (B) during incubation (= Egg) and brood-rearing (= Hatchling) phases, and (C) when roads were present or absent within 1,500 m.

The most parameterized model adequately fit the observed values in the daily nest survival analysis (χ^2 = 2.15, df = 5, P = 0.83). Two models were competitive: sugarcane + phase and sugarcane + road (Table 2). The 95% CI for the odds ratio of sugarcane indicated significance, and the odds ratio value suggested that the odds of a nest surviving from one day to the next was ~8.5× greater when sugarcane was present within 1,500 m of a nest than when it was absent (Table 3 and Fig. 3A). There was a trend toward a lower daily survival rate during the brood-rearing phase than during the incubation phase, but this trend was not significant (Table 3 and Fig. 3B). There also was a trend toward lower daily survival when major roads were near nests than when they were absent, but likewise this trend was not significant (Table 3 and Fig. 3C).

Within-brood survivorship.—The most parameterized model adequately fit the observed values for the within-nest survivorship analysis (χ^2 = 5.22, df = 7, P = 0.63). The model containing the effect of order and the interaction of harvest and age received the strongest support (Table 4). No other models were competitive. Although the model-averaged parameter estimate for order was not significant (Table 5), this parameter was a significant factor ($P < 0.05$) in all individual models in which it was included. The interaction

Table 4. Model fit for analysis of daily survival rates of 84 nestling Barn Owls in the Everglades Agricultural Area (K is the number of model parameters, AIC_c is Akaike's information criterion with a second-order correction for small sample size, ΔAIC_c is the difference between a particular model and the top ranked model, and w_i is the model weight).

Model	K	AIC_c	ΔAIC_c	w_i
Order + harvest*age	6	186.73	0.00	0.990
Harvest + order*age	6	198.48	11.74	0.003
Order + age + harvest	5	198.55	11.81	0.003
Order + age	4	198.64	11.91	0.003
Order*age	5	198.90	12.17	0.002
Harvest*age	5	212.87	26.13	0.000
Order + harvest	4	214.17	27.44	0.000
Order	3	214.82	28.09	0.000
Age + harvest	4	219.77	33.04	0.000
Age	3	221.27	34.54	0.000
Harvest	3	222.90	36.17	0.000
Constant	2	224.45	37.72	0.000

between harvest and age was significant (Table 5). Daily survival rate increased with age in nests surrounded by sugarcane and decreased with age in nests surrounded by harvested fields (Fig. 4). Overall, daily survival was higher in nests surrounded by standing sugarcane but was highly variable in nests surrounded by harvested fields.

Morphological development.—Nestling mass varied significantly depending on whether the nestlings were from preharvest nests and survived to fledge, were from postharvest nests and survived, or were from postharvest nests and died before fledging ($F = 4.26$, df = 2, $P = 0.01$; Fig. 5). Postharvest nestlings that died weighed significantly less than preharvest nestlings and postharvest nestlings that survived to fledge ($t = -2.56$, Bonferroni corrected $P = 0.03$ and $t = -2.44$, $P = 0.04$, respectively). Mass did not differ between preharvest and postharvest nestlings that survived ($t = -0.46$, Bonferroni corrected $P = 1.94$). Tarsus length varied significantly among groups as well ($F = 3.76$, df = 2, $P = 0.02$); however, pairwise differences between groups were not apparent in the Bonferroni comparisons. Wing chord did not vary significantly among any groups ($F = 1.24$, df = 2, $P = 0.29$).

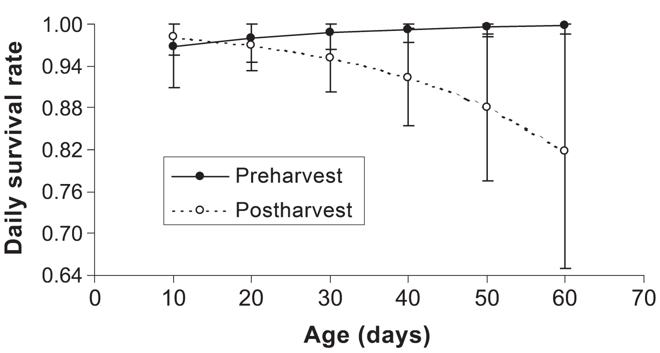

Fig. 4. Daily survival rates (± 95% CI) of nestling Barn Owls by age of nestling when sugarcane was present or absent in the Everglades Agricultural Area in 2006.

Table 5. Model-averaged parameter estimates (± SE) and odds ratio values for predictor variables of daily survival of 84 individual nestling Barn Owls in the Everglades Agricultural Area.

Variable	Model-averaged parameter estimate	Odds ratio	95% CI
Order	−1.03 ± 0.24	0.36	−1.27 to −0.22
Age	−0.10 ± 0.02	0.90	−1.02 to −0.86
Harvest (post- vs. preharvest)	−2.80 ± 1.68	0.06	−5.35 to 0.00
Order*age	0.00 ± 0.00	1.00	1.00–1.00
Harvest*age (post- vs. preharvest)	0.12 ± 0.04	1.13	1.05–1.22

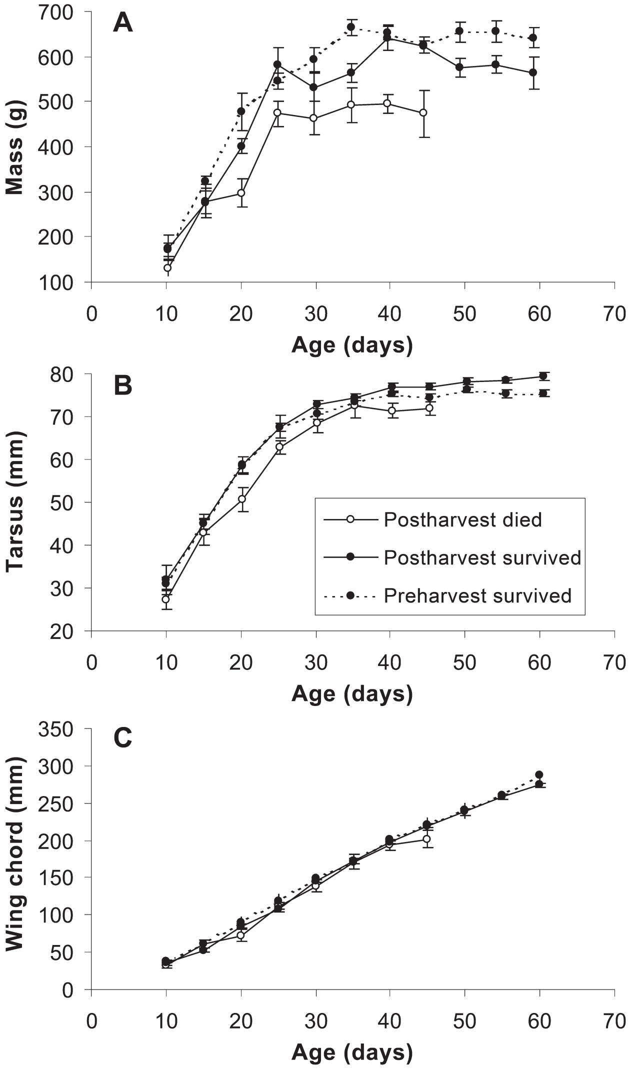

Fig. 5. Growth curves depicting mean (A) mass, (B) tarsus length, and (C) wing chord length (± SE) for nestling Barn Owls in preharvest nests that survived to fledge, in postharvest nests that survived, and in postharvest nests that died before fledging from the Everglades Agricultural Area in 2006.

Discussion

Daily nest survival of Barn Owls in the EAA was negatively related to change in habitat quality within breeding seasons. When most Barn Owls in the EAA select nesting locations, the entire landscape may be considered "good" because harvesting activities have not begun and therefore rodents, their primary food resource, are plentiful and widely distributed. When rodent populations decline following the removal of their food and cover by harvesting, nesting locations of Barn Owls become increasingly isolated from food resources and daily survival rates decline. Once nesting attempts have been initiated, Barn Owls may be unable or unwilling to abandon nests. Although we did not collect long-term demographic data to test for population-level effects, our study demonstrates that the temporal instability of habitat quality inherent in agricultural systems can result in lowered nest success of individual birds. However, that the EAA is an ecological trap for Barn Owls is unlikely given the apparent stability of the population over time (R. N. Raid pers. obs.). Large populations of recruits necessary to support the densities of owls observed in the EAA are not known to exist nearby; therefore, the majority of population replacement likely occurs from within the EAA.

Daily survival rates of Barn Owl nests had greater associated variance when sugarcane was absent. This variability was likely attributable to habitat characteristics not measured in the present study, such as the presence of weedy ditch banks and refuse piles and distance to uncut fields. These types of areas may serve as refugia that allow rodents to persist locally after sugarcane harvest, which then buffers harvest-induced declines in rodent abundance. Another potential source of greater variance associated with postharvest nesting is differences in parental foraging ability. Variation in hunting efficiency may not have been apparent until food resources were relatively scarce in the landscape. Under these conditions, distance to the nearest food source may be more prohibitive for less capable individuals.

Patterns of mortality and change in body mass of individual nestlings support food availability as a key issue in nestling survivorship. Nearly all the nestlings monitored in locations with constant sugarcane cover survived to fledge, whereas ~50% of nestlings located in areas where sugarcane was harvested before the onset of nesting died before fledging. Nestlings that died before fledging from nests where sugarcane had been harvested weighed less than all nestlings that survived to fledge, and when sugarcane was absent, the probability of chick survival decreased with age. However, the likelihood of daily survival of nests of both songbirds and raptors has previously been shown to increase with nest age during the nestling phase (e.g., Dinsmore et al. 2002, Grant et al. 2005, Brown and Collopy 2008). Although some nestling mortality may have been linked to parental mortality associated with roads, starvation was likely the primary source of nestling death.

Monitoring of nestlings in pre- and postharvest nests was unavoidably correlated with date, so the observed differences in survival of nestlings could have been related to temporal factors other than sugarcane harvest. However, this is unlikely because of the enormous impact of sugarcane harvest on rodent abundance, which likely overwhelms any seasonal variation in rodent abundance in the EAA (Martin 2009). The high reliance of Barn Owls on rodents as a food source, the large changes in rodent populations during the sugarcane cropping cycle, and the association of nestling growth and mortality with the presence or absence of sugarcane suggest a strong link between sugarcane harvest and the reproductive success of Barn Owls.

The present study highlights the need to consider how the influence of habitat may shift over time when evaluating how specific habitat variables influence the nest success of birds and, ultimately, how these factors influence populations of birds as a whole. By identifying factors that contribute to nesting success but are also susceptible to short-term change, it may be possible to prevent or delay shifts in habitat quality until nesting has been completed. In the case of Barn Owls in the EAA, delaying harvest of sugarcane fields adjacent to occupied nest boxes until after nestlings have fledged would likely maximize the likelihood of daily nest survival by ensuring the availability of food for nestlings.

Because Barn Owls are declining in many parts of the United States, a highly productive population of this species in the EAA may contribute to the stability of the wider regional population by providing recruits that disperse throughout the surrounding landscape. Little is known about dispersal patterns of juvenile Barn Owls, but dispersal distances of up to 2,000 km have been recorded (Stewart 1952, Soucy 1980). This topic merits further study; meanwhile, efforts should be made to maximize the reproductive output of Barn Owls in the EAA.

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