

The effects of nesting success and mate fidelity on breeding dispersal in burrowing owls

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Abstract: Understanding and describing the factors that affect avian breeding dispersal is critical for modeling population dynamics and designing conservation strategies. We investigated the hypothesis that dispersal probability and dispersal distance is affected by nesting success and mate fidelity with band-resight data (1998-2003) from burrowing owls (*Athene cunicularia* (Molina, 1782)) nesting in southern California. Most owls (167 of 253, 66%) remained near their initial nest (< 100 m), and those that moved > 100 m dispersed an average of 472 ± 65 m ($n = 86$; mean \pm 1 SE). Both female and male owls whose nests failed were more likely to disperse and dispersed longer distances than owls with successful nests. Failed nesting attempts were also associated with an increased probability of divorce, and divorce was related to increased dispersal probabilities and distances. Moreover, female and male owls tended to be more likely to disperse and to disperse greater distances following the death of a mate than those that remained paired. Although dispersal was related to mate fidelity, nesting success remained an important factor affecting dispersal even after controlling for the effects of mate loss. Our results suggest that nesting failure was the primary factor associated with dispersal probability and dispersal distance in burrowing owls in our population.

Introduction

Breeding dispersal, defined as the movement of adults between breeding attempts, is an important life-history characteristic that can have significant effects on individual fitness as well as population dynamics (Greenwood and Harvey 1982; Johnson and Gaines 1990). Current theory suggests that in some cases, dispersal is a means to increase subsequent reproductive success, and many studies have found an association between reproductive failure and increased breeding dispersal (Wiklund 1996; Gowaty and Plissner 1997; Haas 1998). In contrast, remaining with a mate or on a territory may be beneficial because familiar pairs may have higher reproductive success than unfamiliar pairs (Schieck and Hannon 1989), and increased dispersal distances may result in reduced reproductive success following dispersal (Dow and Fredga 1983; Schieck and Hannon 1989). The effect of mate fidelity is further shown by the increase in dispersal probability and distance following the death of a mate (Murphy 1996; Wiklund 1996; Millsap and Bear 1997). In these cases, mate fidelity and the benefits of nest site fidelity (previous experience at a breeding site) act to reduce breeding dispersal, potentially in opposition to the effects of nesting failure, suggesting that both dispersal and philopatry may increase subsequent nesting success, so that an optimal strategy is unclear.

Differentiating between the effects of nesting success, mate fidelity, and nest site fidelity is difficult because of their close association with one another (Greenwood and Harvey 1982; Cézilly et al. 2000; Beheler et al. 2003). Nesting failure could be related either to a territory or to a mate (Goodburn 1991), which could affect mate fidelity (Choudhury 1995; Dubois and Cézilly 2002) as well as nest site fidelity. Moreover, the factors that affect dispersal probability may differ from those that affect dispersal distance (Forero et al. 1999; Serrano et al. 2001). Despite these complications, recent studies have attempted to deal with the effects of mate fidelity and

nesting success on dispersal (Forero et al. 1999; Beheler et al. 2003), the effects of habitat and environmental quality on dispersal (Serrano et al. 2001; Byholm et al. 2003), and how these effects may differ between dispersal probability and dispersal distance (Forero et al. 1999; Serrano et al. 2001; Byholm et al. 2003).

We examined patterns of avian breeding dispersal in relationship to nesting success, mate fidelity, and nest site fidelity in burrowing owls (*Athene cunicularia* (Molina 1782)) to evaluate the relative importance of these factors to avian dispersal. We hypothesized that dispersal probability and dispersal distance would be greatest for owls whose nests failed, owls that did not remain paired, and owls without previous experience at a nest site (nest site fidelity). In addition to examining the direct effects of nesting success and mate fidelity on dispersal, we hypothesized that failed nesting attempts would be associated with higher rates of divorce. The burrowing owl is a Species of Special Concern in California and has been declining in parts of its North American range (Haug et al. 1993; Klute et al. 2003). Their dispersal behavior, however, is poorly understood (but see Millsap and Bear 1997; Lutz and Plumpton 1999). Understanding dispersal will be vital in evaluating the owl's ability to reestablish declining or extirpated populations.

Methods

Study Area

We conducted our study in the Imperial Valley, California, south of the Salton Sea, ca. 40 km north of El Centro, California (33° 07' N, 115° 31' W). The area was characterized by intensive agriculture and a high density (8.3 pairs km⁻²) of non-migratory burrowing owls with highly variable reproductive success among years (Rosenberg and Haley 2004). Owl nests were found

primarily along the water delivery system surrounding the agricultural fields. This system consisted of cement ditches and canals, as well as earthen drains, all of which provided nesting habitat for the owls (Rosenberg and Haley 2004).

Band Application and Resighting

We banded adult and juvenile burrowing owls during the 1998–2002 breeding seasons (April–July) and relocated banded owls during the 1999–2003 breeding seasons. Owls were banded within a central area, the Intensive Study Area (ISA; ca. 11.7 km²). We fitted each bird with a colored, metal alpha-numeric band (Acraft Sign and Nameplate Co., Canada) and a USGS numeric metal band (size 4). We relocated banded birds each year using two surveys from a truck within the ISA, and adjoining lands of the Sonny Bono Salton Sea National Wildlife Refuge (hereafter Refuge), and an area 0.8 km beyond these areas (area B). Surveys were performed at speeds ≤ 10 km h⁻¹ along all of the roadways and waterways within the ISA, Refuge, and area B. The two surveys occurred at the beginning of the breeding season and were augmented with incidental relocations throughout the breeding season. Owl nests were monitored throughout the breeding season to determine the identity of all owls as well as the success of each nesting attempt. These survey methods resulted in a detection probability within the ISA and area B of 1.0 for male owls and 0.91 for female owls (Rosenberg and Haley 2004). We also performed a single driving survey 0.8 km (1999) and 1.6 km (2000–2003) beyond area B during the breeding season. Some authors have expressed concern over using band resight data to estimate dispersal distributions because a negative bias could be present if the subjects disperse beyond the search boundaries of the study (Porter and Dooley 1993; Koenig et al. 1996). Prior analyses of dispersal (Rosenberg and Haley 2004) and data from a concurrent

radio-telemetry study (Catlin 2004) allowed us to assume that few owls (1 of 14; ca. 7%) disperse beyond that study area.

Statistical Analyses

Data. We only included owls whose previous year's nesting success was known. We used the straight-line distance between an owl's previous nest and its current nest to represent dispersal distance. Owls whose previous year's nests were known to be destroyed by road or waterway maintenance activities were also excluded from analyses. This type of nest failure precludes the reuse of a nest burrow. Furthermore, it appears that the reaction of owls following nest destruction may differ from that of owls that fail to breed for other reasons (Catlin and Rosenberg, in press).

Dispersal Probability. We treated dispersal probability and the subsequent dispersal distance as separate events because they may be affected by different factors (Forero et al. 1999; Catlin 2004). We defined dispersal as movements of 100 m or greater from the previous nest site between breeding seasons. One hundred meters was approximately the median nearest neighbor distance for active burrowing owl nest sites at our study area (Rosenberg and Haley 2004) and contains the area around a nest that includes satellite burrows for juveniles and the breeding pair (Desmond and Savidge 1999; Ronan 2002), as well as a critical distance for competition between neighboring breeding pairs (Green and Anthony 1989). In addition, within this study, owls whose nests failed in the previous year moved either ≤ 16 m (32%) or ≥ 117 m (68%), whereas owls that successfully nested did not show this bimodal behavior (see **Results**), supporting our use of the 100 m criteria for dispersal.

We examined models of dispersal probability (between years t and $t + 1$) that included variables for nesting success in year t (at least one nestling survived to ≥ 21 –28 days), year, nest site fidelity, and mate fidelity. Nest site fidelity referred to previous experience at a breeding site (in year $t - 1$) and thus covered a three-year period; the nest site fidelity variable received a one if an owl nested at that site (≤ 100 m) the previous year and zero otherwise. Mate fidelity was defined as retaining a mate between breeding seasons (between years t and $t + 1$); owls that bred with a new mate in year $t + 1$ were classified as “widowed” if their mate was missing from the study area (presumed dead) and “divorced” if their mate was known to be on the study area. We used logistic regression (PROC LOGISTIC, SAS 2001) to evaluate the relationships between the variables and dispersal probability. The estimates presented from logistic regression analyses represent back-transformed log-odds ratios. We developed three models for dispersal probability because data were not available for mate fidelity and nest site fidelity for all owls (Table 1). The effect of year was estimated using the model with the largest sample size (Table 1). Models of dispersal probability with mate fidelity as a variable did not include a separate variable for divorced owls because all divorced female owls had dispersed, and the parameters in the model could not be estimated with logistic regression (Allison 1999). Instead, we combined owls that were not with their mate into a single variable that represented being with or without a mate in year $t + 1$.

Dispersal Distance. The models for dispersal distance (between years t and $t + 1$) were the same as those for dispersal probability (Table 1). We used multiple linear regression (PROC GENMOD, SAS 2001) to assess the relationships between the explanatory variables and the log transformation of distance dispersed. The estimates presented from multiple linear regression represent the multiplicative change in median distance associated with a variable. Unlike the

dispersal probability models, divorced owls were included separate from widowed owls in the analyses (Table 1).

Nesting Success and Mate Fidelity. There is some evidence that nesting failure and divorce are related (Choudhury 1995; Dubois and Cézilly 2002), which may confound the relationship between the two variables and dispersal. We performed a Fisher's exact test on mate fidelity (whether a pair remained intact or divorced between years t and $t + 1$) in response to nesting success (in year t) in an effort to clarify this relationship. Furthermore, we examined collinearity in the dispersal distance models where divorce and nesting success appeared as explanatory variables to ensure that our estimates were not affected by a relationship between the two variables. The values for statistical measures of collinearity (condition indices, tolerance, and variance inflation factors; Belsley 1990) suggested that collinearity was not an issue in our sample, which allowed us to include both nesting success and divorce as variables in our models that examined dispersal distance (Table 1). All regression estimates are presented with 95% confidence intervals, and all analyses were performed separately for each gender.

Results

Both female and male owls exhibited fidelity to nest sites, both in terms of dispersal probability and dispersal distance. Many owls (167 of 253, 66%) remained within 100 m of their previous nest, and most of those that dispersed remained within 400 m of their original burrow (59 of 86, 69%). From 1998 to 2003, 37 of 101 (37%) female owls and 49 of 152 (32%) male owls whose nesting success was known dispersed. The average distance dispersed by female and male owls was 526 ± 121 m and 431 ± 68 m, respectively (Table 2).

Nesting Success and Dispersal

Dispersal Probability. Nesting success appeared to be the primary factor associated with dispersal probability. Both female and male owls whose nests failed were more likely to disperse; 11 of 15 (73%) female owls with failed nests dispersed, and only 26 of 86 (30%) female owls with successful nests dispersed. Similarly, 17 of 26 (65%) male owls with failed nests dispersed, while 32 of 126 (25%) male owls with successful nests dispersed. The parameter estimates from these models offered further evidence that nesting failure increased dispersal probability (female: log odds ratio, 6.5, 95% CI: 1.7–24.0, $P < 0.01$, male: 7.0, 95% CI: 2.7–18.7, $P < 0.001$). Dispersal probability did not vary by year (female: $P = 0.52$, male: $P = 0.31$).

Dispersal Distance. Nesting success had a strong effect on dispersal distance; owls whose nests had failed dispersed greater distances than owls whose nests were successful (Table 2, Figure 1). The parameter estimates clearly indicated that nesting failure was associated with increased dispersal distance in both genders (female: 1.9, 95% CI: 1.1–3.5, $P = 0.03$, male: 1.6, 95% CI: 1.1–2.5, $P = 0.02$). Dispersal distance did not vary by year (female: $P = 0.84$, male: $P = 0.13$).

Nest Site Fidelity and Dispersal

Dispersal Probability. There was little evidence that owls with previous breeding experience at a nesting site were more likely to remain at a nest site than those that did not have previous experience. Four of 23 (17%) female owls that previously bred at the same nesting site dispersed, while seven of 17 (41%) female owls that did not have previous experience dispersed. Male owls that were previously site faithful had a similar dispersal probability (21 of 65, 32%) as

male owls that did not have previous experience at a nest site (11 of 28, 39%). The parameter estimates were consistent with the hypothesis that nest site fidelity was associated with decreased dispersal probability but were statistically non-significant (female: log odds ratio, 0.3, 95% CI: 0.1–1.6, $P = 0.17$, male: 0.7, 95% CI: 0.3–2.1, $P = 0.54$).

Dispersal Distance. Despite some apparent differences in the distances dispersed between owls with and without previous experience at a breeding site (Table 2) there was little evidence from the models that experience affected dispersal distance (female: 1.0, 95% CI: 0.4–2.6, $P = 0.99$, male: 1.4, 95% CI: 0.9–2.2, $P = 0.18$).

Mate Fidelity and Dispersal

We were able to determine the between-year mate fidelity of 272 owls (136 pairs) from 1998–2003. Of these, 114 owls (42%) remained with their mate between breeding seasons, 74 owls (27%) were presumed dead, 74 owls (27%) were widowed, and 10 owls (4%) were known to be divorced.

Dispersal Probability. Mate loss through death and divorce appeared to increase dispersal probability. Of the 114 owls that remained paired between breeding seasons, 28 (25%) dispersed. In contrast, all of the five (100%) divorced female owls dispersed, and four of five (80%) divorced male owls dispersed, indicating that divorce and dispersal were closely related in both male and female owls. Of owls whose mate died, 11 of 23 (48%) female owls and 19 of 51 (37%) male owls dispersed. The parameter estimates suggested that mate loss through death or divorce was associated with increased dispersal probability, but the evidence was statistically weaker for male owls (female: log odds ratio, 3.0, 95% CI: 1.1–8.7, $P = 0.04$, male: 1.9, 95% CI: 0.8–4.6, $P = 0.14$).

Dispersal Distance. Similar to dispersal probability, the loss of a mate through death or dispersal was associated with increased dispersal distances (Table 2). The parameter estimates for both genders were consistent with the hypothesis that mate loss increased dispersal distance; however, results were statistically weak (female [dead: 1.7, 95% CI: 0.9–3.1, $P = 0.08$, divorced: 1.3, 95% CI: 0.5–3.2, $P = 0.63$], male [dead: 1.2, 95% CI: 0.8–1.9, $P = 0.43$, divorced: 1.8, 95% CI: 0.8–4.1, $P = 0.18$]).

Nesting Success and Mate Fidelity. Because of a possible relationship between nesting success and mate fidelity, we attempted to describe this relationship as well evaluate the effect of including both variables in the model of dispersal probability and distance. Mate fidelity was related to nesting success, in terms of divorce. Of the five pairs of owls that divorced, four of them had a failed nesting attempt in the previous year; pairs whose nests failed were more likely to divorce than pairs whose nests succeeded (Fisher's exact two-sided P -value, $P < 0.001$, $n = 62$). After accounting for the effects of mate fidelity through its inclusion in the regression model (Table 1), nesting success still affected dispersal probability and dispersal distance. In this case, male owls were more likely to disperse following nest failure, but the effect was less significant for female owls (females: log odds ratio, 3.3, 95% CI: 0.8–14.1, $P = 0.10$, males: 5.9, 95% CI: 1.7–20.8, $P < 0.01$), similar to the results without both variables. Nesting failure, however, appeared to increase the median dispersal distance in both genders after controlling for mate fidelity (females: 2.3, 95% CI: 1.1–3.2, $P = 0.03$, male: 1.9, 95% CI: 1.1–3.3, $P = 0.03$), suggesting that the effect of nesting success was separate from the effect of mate fidelity.

Discussion

While nesting success, mate fidelity, and nest site fidelity all were associated with burrowing owl breeding dispersal, the ways in which they affected dispersal differed and offered insight into the contribution of these factors to dispersal. Nesting failure was the major factor associated with increased burrowing owl dispersal probability and distance, consistent with the avian literature (Wiklund 1996; Gowaty and Plissner 1997). Experimental nest failure has been shown to increase the probability of dispersal in American robins (*Turdus migratorius* Linnaeus, 1766), brown thrashers (*Toxostoma rufum* (Linnaeus, 1758)), and burrowing owls (Haas 1998; Catlin 2004). In addition, Lutz and Plumpton (1999) found that female burrowing owls with larger broods in the previous year were more likely to return to their former nest sites. These dispersal responses should be associated with two factors that contribute substantially to nest failure: mate and habitat quality (Goodburn 1991). If so, dispersal would reflect an attempt to increase future productivity by dispersing to a better territory or a better mate. When mate fidelity was accounted for in the models, the effect of nesting success remained, particularly for male owls, indicating that nesting failure affected dispersal probability and distance regardless of the presence of a mate. For female owls, some of the variation in dispersal probability associated with nesting failure may have been attributable to mate loss; evidence in support of an effect from nesting failure decreased when mate fidelity was in the models, but small sample sizes for females may have decreased our power to detect a difference. As predicted, divorce was related to nesting failure, indicating that owls were both more likely to disperse and to change mates following reproductive failure. Theory suggests that individuals may be able to improve their reproductive prospects by changing mates between breeding seasons (Choudhury 1995). Our dispersal results indicate that nesting failure may be related to both mate and territory quality in

burrowing owls; a direct connection between fitness and these factors, however, remains to be estimated.

Previous experience at a breeding site did not appear to affect burrowing owl dispersal directly. We found similar philopatry rates (66%) as those reported in the literature for other raptors; 70% of black kites (*Milvus migrans* (Boddaert, 1783); Forero et al. 1999) and 72% of lesser kestrels (*Falco naumanni* Fleischer, 1818; Serrano et al. 2001) remained faithful to breeding territories between breeding seasons. Our rates were lower than a resident population of burrowing owls in central Florida ($\geq 74\%$, Millsap and Bear 1997) but very similar to a migratory population of burrowing owls nesting in black-tailed prairie dog (*Cynomys ludovicianus* (Ord, 1815)) towns in Colorado (66%, Plumpton and Lutz 1993; $\geq 63\%$ Lutz and Plumpton 1999). High nest site fidelity could reflect benefits from breeding with a familiar mate (Schieck and Hannon 1989), the potential of reduced breeding success following dispersal (Dow and Fredga 1983; Schieck and Hannon 1989), or a response to limited burrow availability.

The high mate fidelity observed during the study also supports a hypothesis of increased success among owls with familiar mates; of 62 pairs of owls where both mates were known alive in the subsequent year, five (8%) were divorced. This high mate fidelity was also similar to that observed in the central Florida population; 9% of pairs were divorced (Millsap and Bear 1997). Increased dispersal probability and dispersal distance were associated with divorce in our population, but the low incidence of divorce suggests that mortality was the major factor contributing to mate change, similar to results reported by Beheler et al. (2003). The death of a mate was only weakly associated with increased dispersal probability in male owls, indicating that they exhibit some nest site fidelity in the absence of their mates. The evidence that female owls were more likely to disperse following the death of a mate was stronger than that for male

owls, which is similar to other studies (Schieck and Hannon 1989; Murphy 1996; Millsap and Bear 1997) and is consistent with the theory that male birds are more philopatric because they select and defend territories (Wolff and Plissner 1998). Millsap and Bear (1997) suggested that these differences might reflect the importance of male territorial experience. Our results suggest that it may be more difficult to disperse and remain paired, especially when dispersing relatively great distances, implying that burrowing owl mate fidelity is associated with nest site fidelity and decreased dispersal distance. Similarly, Wiklund (1996) found that merlins (*Falco columbarius* Linnaeus, 1758) that remained paired between breeding seasons dispersed shorter than average distances. This relationship agrees with the hypothesis that there is a positive correlation between mate fidelity and nest site fidelity (Cézilly et al. 2000). Overall, however, nesting success was a better descriptor of dispersal distance than mate fidelity in our study.

Our results highlight the importance of nesting success to dispersal and to mate fidelity as well as the relationship between nest site fidelity and mate fidelity. Burrowing owls at our site exhibited high fidelity to nest sites and mates, but nesting success appeared to have the greatest effect on dispersal between breeding seasons, suggesting that they may raise their subsequent reproductive success through increased dispersal probability and distance following nesting failure. Further study on the reproductive consequences of breeding dispersal is necessary to evaluate this hypothesis.

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Figure Legends:

Figure 1: Distribution of adult burrowing owl (*Athene cunicularia*) between-year dispersal distances in the Imperial Valley, California (1998-2003), separated by nest success for female (a) and male (b) owls. Data are presented as the proportion of owls that dispersed a distance within a given interval. The bar for the interval 0-100 m represents owls that did not disperse, according to our definition of dispersal.

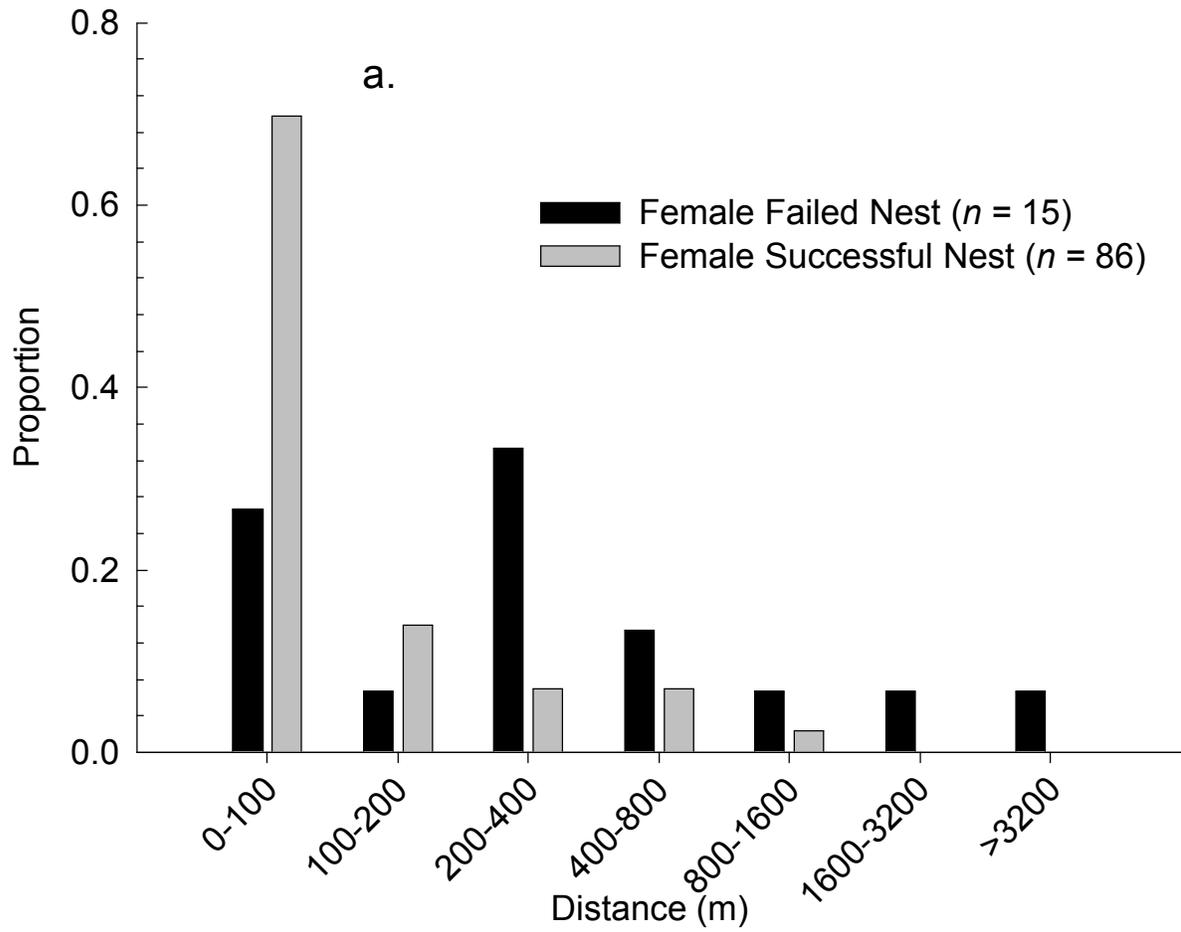


Fig. 1a. Catlin et al.

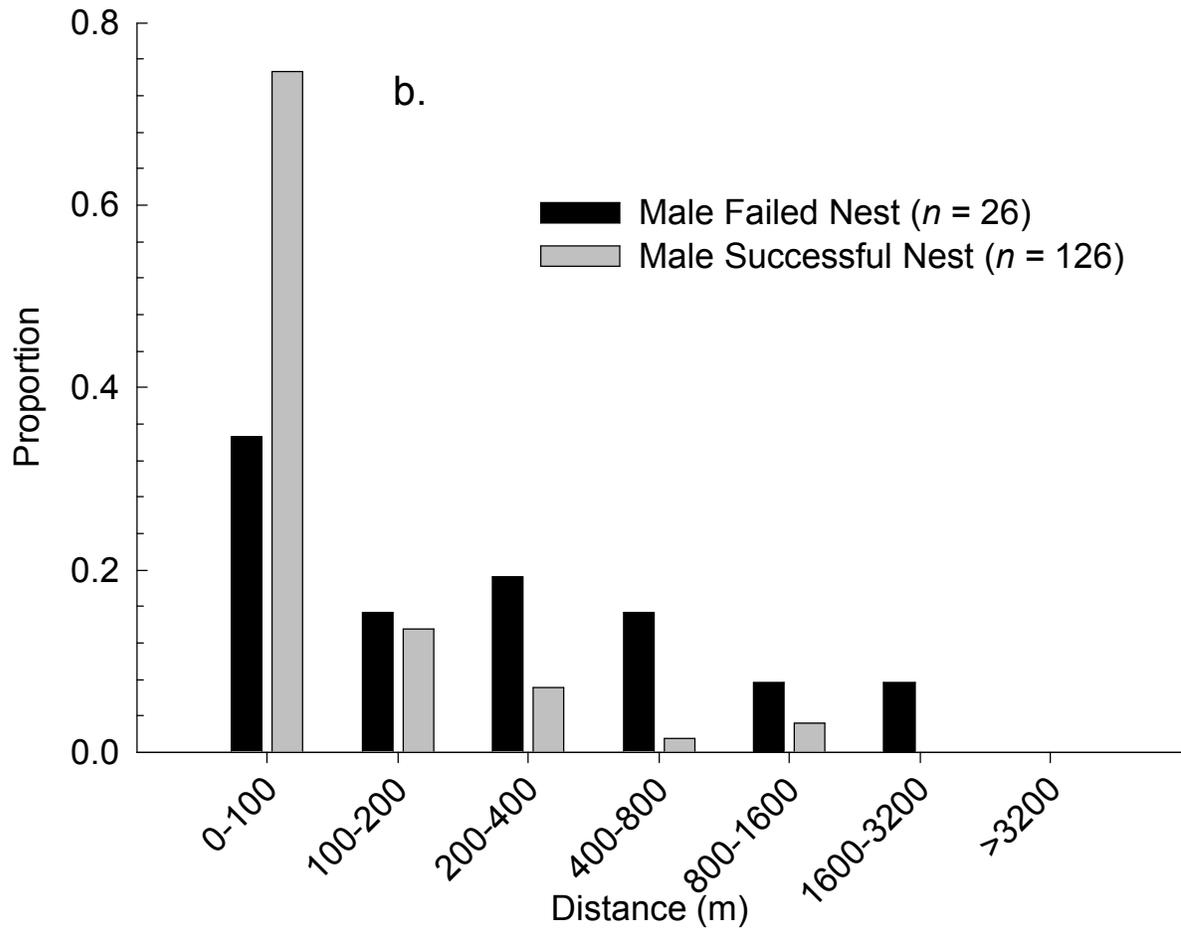


Fig. 1b. Catlin et al.

Table 1: Models and sample sizes for each gender used in examining dispersal probability and dispersal distance of burrowing owls (*Athene cunicularia*) in the Imperial Valley of California.

Model	Female Owls		Male Owls	
	Dispersal	Dispersal	Dispersal	Dispersal
	Probability	Distance	Probability	Distance
SUCCESS + YEAR	101	37	152	49
SUCCESS + NEST SITE FIDELITY ^a + YEAR	40	11	93	32
SUCCESS + WITH MATE ^b + YEAR	85	NA	113	NA
SUCCESS + MORTALITY + DIVORCE + YEAR ^c	NA	30	NA	37

^a Nest site fidelity refers to whether an owl had bred in the same nest site in year t-1.

^b With Mate is a variable combining divorce and the loss of a mate through mortality. This model was used to examine the relationship between nesting success, mate fidelity, and dispersal probability only.

^c This model was used to examine the relationship between nesting success, mate fidelity, dispersal distance only and had separate variables for loss of a mate through divorce and mortality.

Table 2: Comparison of between-year breeding dispersal distances (m) by burrowing owls in the Imperial Valley, California. Data were collected by resighting banded birds during the 1999-2003 breeding seasons. Includes all owls that moved > 100m between breeding seasons.

A. Female Owls ($n = 37$)

		Parameter						
		Nesting Success		Mate Fidelity			Nest Site Fidelity ^a	
	Pooled	Success	Fail	Divorced	Widowed	Paired	Yes	No
	($n = 37$)	($n = 26$)	($n = 11$)	($n = 5$)	($n = 11$)	($n = 14$)	($n = 4$)	($n = 7$)
Mean	526	357	924	976	681	293	283	431
SE	121	54	371	542	301	78	112	147
Range	133–3652	133–1207	194–3652	148–3089	143–3652	133–1207	133–607	143–1207
Median	271	234	396	478	396	186	196	196

^a Nest site fidelity refers to whether an owl had bred in the same nest site in year t-1.

Table 2 (Continued)B. Male Owls ($n = 49$)

		Parameter						
		Nesting Success		Mate Fidelity			Nest Site Fidelity	
	Pooled	Success	Fail	Divorced	Widowed	Paired	Yes	No
	($n = 49$)	($n = 32$)	($n = 17$)	($n = 4$)	($n = 19$)	($n = 14$)	($n = 21$)	($n = 11$)
Mean	431	326	629	1114	382	293	425	294
SE	68	50	166	585	56	78	124	81
Range	101–2771	101–1207	117–2771	226–2771	101–970	133–1207	117–2771	101–970
Median	258	187	373	730	341	186	258	183