Breeding Dispersal and Nesting Behavior of Burrowing Owls Following Experimental Nest Predation

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ABSTRACT.—Nest predation is considered a primary factor affecting the life-history characteristics and particularly dispersal of many avian species. We tested the hypothesis that nest predation would increase dispersal probability, dispersal distance and the frequency of renesting. We removed eggs from burrowing owl (*Athene cunicularia*) nests to simulate nest predation in southeastern California. Owls responded to egg removal with increased dispersal probability, nesting attempts and egg production. We found that nest predation tended to increase dispersal probability (50% depredated nests vs. 14% control nests), which occurred fairly soon after nest predation (0–25 d). Dispersal distance was highly variable among owls (range: 148–13,012 m). Following experimental nest predation, burrowing owls increased the number of nesting attempts and thus the total number of eggs produced in a season, regardless of dispersal. Clutch size, however, decreased as the number of breeding attempts increased. Despite large initial clutch size, burrowing owls in the Imperial Valley may have adapted to nest predation by both dispersal and the ability to renest frequently.

INTRODUCTION

Much of the work in avian dispersal has focused on natal and adult dispersal between breeding seasons (Greenwood and Harvey, 1982), but the amount of empirical and theoretical knowledge has steadily increased for within-season dispersal, particularly in terms of the relationship between dispersal and nest predation (*e.g.*, Jackson *et al.*, 1989; Howlett and Stutchbury, 1997; Powell and Frasch, 2000). Factors such as nest failure can promote breeding dispersal (Greenwood and Harvey, 1982), and nest failure due to predation has been cited as a primary factor promoting avian dispersal both within and between breeding seasons (Greig-Smith, 1982; Jackson *et al.*, 1989; Haas, 1998; Hakkarainen, 2001), especially in the case of a predator that revisits nests (Sonerud, 1985). Studies predict that dispersal may be a means to avoid further nest predation (Sonerud, 1985; Powell and Frasch, 2000). Longer distance movements, however, may not reduce the probability of subsequent nest predation (Greig-Smith, 1982; Powell and Frasch, 2000). This point raises the question of what, if any, benefit there may be to dispersal following nest predation, especially when multiple nest attempts are possible.

Multiple breeding attempts in a single season are common among many birds, regardless of nesting success (Martin, 1995). Nest predation in particular, appears to have significant effects on nesting and renesting in some birds, including the timing and success of subsequent attempts (Slagsvold, 1984; Martin, 1995), as well as clutch size in subsequent years (Doligez and Clobert, 2003). Small clutch size may be an adaptation to nest predation because it allows for frequent renesting at small costs to fitness (Slagsvold, 1982, 1984). Although renesting attempts may produce diminished returns (Kershner *et al.*, 2001), such attempts appear to increase individual fitness (Martin *et al.*, 1989; Hipfner, 2001).

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Theory suggests species with large clutch sizes evolved in environments with low nest predation rates (Slagsvold, 1982, 1984) and that some species limit nest predation through nesting strategies such as hole nesting (von Haartman, 1957). The burrowing owl (*Athene cunicularia*) provides an ideal subject to evaluate how species with large clutch sizes (up to 14 eggs, Todd and Skilnick, 2002) and the ability to renest frequently (Catlin, 2004) respond to nest predation. The burrowing owl is a small ground-dwelling owl widely distributed throughout western North America, Florida, Central and South America and on several islands in the Caribbean (Haug *et al.*, 1993; Clark, 1997). Despite large clutch sizes, variable reproductive success and a relatively low survival rate (0.62–0.65; Rosenberg and Haley, 2004) should increase the likelihood that burrowing owls will renest within a breeding season following an initial failure, resulting in the potential for within-season breeding dispersal. Indeed, burrowing owls are capable of long distance dispersal within a breeding season following nesting failure (Rosier *et al.*, 2006).

We examined the effects of experimental nest predation on within-season dispersal and nesting behavior in a population of burrowing owls nesting in an agricultural environment, characterized by low nest predation rates (Haley, 2002; Rosenberg and Haley, 2004). We hypothesized that nest predation would increase the probability and distance of within-season dispersal.

METHODS

STUDY AREA

Our study site was located in the Imperial Valley within the Sonny Bono Salton Sea National Wildlife Refuge Complex and adjacent private agricultural lands in southeastern California. The study area is within the Colorado Sonoran Desert region, characterized by extreme summer temperatures and low precipitation (Molina and Shuford, 2004). It is an intensive-use agricultural region, supporting changing crops throughout the year. Natural owl burrows and artificial owl nest boxes existed primarily along canals and drains within the agricultural matrix (Haley, 2002; Rosenberg and Haley, 2004). Potential nest predators in this valley include gopher snakes (*Pituophis catenifer*), striped skunks (*Mephitis mephitis*) and badgers (*Taxidea taxus*; Coulombe, 1971).

FIELD TECHNIQUES

Radio application.—We used radio-telemetry to estimate within-season dispersal probability and distance. We trapped breeding owls during the 2002 breeding season (Apr. to Aug.) within an 11.7 km^2 central portion of the study area, using spring-loaded traps and 2-way burrow traps (Rosenberg and Haley, 2004). Owls were fitted with radio transmitters that had a ca. 400-d battery life (American Wildlife Enterprises, Monticello, Florida), a harness mount and a total assembly weight of 5.08 ± 0.02 g (mean values are presented as mean ± 1SE; n = 36).

Experimental predation.—We identified potentially active nests using behavioral observations. Each of these potential nests, regardless of future designation as experimental or control, was checked weekly using an infrared probe (Sandpiper Technologies, Manteca, California); the final designation as a nest was based on observing eggs. The infrared probe was used for several years and at several sites, and there was no indication that its use affected nest success (D. K. Rosenberg, pers. obs.) Eighteen nests were included as experimental and control units. To ensure that experimental and control treatments were distributed equally in time and space, we paired nests by location and timing and randomly assigned one to the experimental group and the other to the control group. We removed eggs from experimental nests

following clutch completion and attempted to remove each subsequent clutch throughout the season. Eggs were used for a toxicological study (Gervais and Catlin, 2004) or were deposited in the egg collection of the Western Foundation of Vertebrate Zoology (Camarillo, California). The control nests were visited in the same fashion and for the same amount of time as the experimental nests, but the clutches were left intact and untouched. All of the owls used in the analyses initially nested in artificial burrows.

Owl relocation.—We used ground and aerial surveys to locate radio-tagged owls. The receiving antenna was mounted to the bed of a truck and consisted of two 4-element Yagi antennae (Cushcraft Corp., Manchester, New Hampshire) joined by a null combiner (Telonics, Inc., Mesa, Arizona; Gervais *et al.*, 2003). The ground surveys started at the last known location of each owl, but if we were unable to locate a radio-tagged owl at this location, we covered a 1 km diam circle, checking at 500-m increments in each of the four cardinal directions around the last known location. After we located an owl via radio-telemetry, we attempted to confirm visually the owl's status (alive, dead, renesting). In the case of owls that were found in the nest burrow, we used the infrared probe to confirm the status at each weekly interval. We searched for owls that could not be located using the ground methods with aerial surveys from a fixed-wing aircraft. We consistently searched an area of ca. 2250 km^2, providing a maximum area of detection of ca. 23–27 km from the central study area. The same north-south aerial transects with 5 km spacing were performed approximately every 2 wk throughout the 2002 breeding season. The locations of all experimental and control owls were known by the end of the breeding season.

Dispersal.—Although the minimum distance used to determine dispersal is arbitrary, the factors affecting dispersal probability and dispersal distance may be different (Forero *et al.*, 1999), justifying an attempt to define dispersal. For owls for which we knew where each subsequent nesting attempt occurred, we defined dispersal as a movement of >100 m from its previous nest. 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 has been cited in other studies as the area around a nest that includes satellite burrows for the breeding pair as well as a critical distance for competition between neighboring pairs (Green and Anthony, 1989; Ronan, 2002). For owls that either did not renest, or for which we could not confirm renesting, we considered a bird to have dispersed if it was found >100 m from its nest for at least 3 wk and to have been <100 m from its new burrow during the following three weekly checks. We used a minimum of three weeks as a criterion for dispersal because the mean number of days between experimental clutch collection and clutch completion for experimental renesting attempts was approximately 21 d (*see* results). If an owl was >100 m from its nest for at least three weeks and did not settle at a new burrow within the breeding season (prior to the last week in Aug.) or prior to death, the owl was classified as a wanderer. Owls classified as wanderers, or that did not survive ≥28 d after transmitters were attached, were excluded from analyses. Owls that renested <100 m from their previous nest or that remained within 100 m of their previous nest without renesting until the end of the breeding season or until death were classified as non-dispersers. If the exact location of the burrow to which an owl dispersed was not known, dispersal distance was calculated by averaging the weekly distance from the initial nest.

<div align="center">STATISTICAL ANALYSES</div>

From the 36 owls (nine experimental pairs, nine control pairs), we did not include 14 owls in the analysis because of early mortality, nest destruction by road maintenance, natural nest predation, our inability to capture several mates and one owl that continued to move before its death (Catlin, 2004). Control nests acted as controls against our removal of eggs

and were not excluded if they failed for reasons other than nest predation. This resulted in 22 owls from 15 nests (eight experimental and seven control) that were radio-harnessed and included in the analyses.

We separated dispersal behavior into dispersal probability and distance. These events are likely separate decisions by the owls and could be related to different causative factors (Forero *et al.*, 1999). We used a one-sided Fisher's exact test to evaluate the effects of experimental nest predation on dispersal probability. The response was positive if at least one owl from a pair dispersed and negative if none dispersed. We only used the reaction of the pairs following removal of the first clutch. We also calculated summary statistics for dispersal probability, dispersal distance and timing of dispersal. We did not analyze dispersal distances because only one control owl dispersed. The timing of dispersal represented the number of days following experimental predation before an owl dispersed. The date of dispersal was calculated as the midpoint between the last date an owl was located at its initial nest during our weekly radio searches and the date of the subsequent search when the owl was not found, found between nesting sites, or found at its new nesting site. We also present summary statistics (means, SE and range) on time between experimental predation and renesting and clutch size for experimentally depredated owls.

RESULTS

DISPERSAL

The effects of experimental nest predation on within-season dispersal were consistent with our predictions. Dispersal probability was much higher for owls from experimentally depredated nests (45%, five of 11 owls), than for owls from control nests (9%, one of 11 owls). At least one owl from a pair dispersed in four of eight (50%) experimental pairs and in one of seven (14%) control pairs. Despite the large difference between dispersal rates (50 vs. 14%), the small number of pairs resulted in statistically non-significant differences (Fisher's exact one-sided p-value, P = 0.18, n = 15 pairs). The one control owl that dispersed was a female owl that abandoned its nest with the clutch apparently intact; the owl's subsequent nesting attempt was successful. In terms of dispersal distance, reaction to nest predation was highly variable (mean = 2802 ± 2553 m, range: 148–13,012 m, n = 5). The one control owl that dispersed moved 1575 m following abandonment of her first clutch. Dispersal distances for known renesting attempts of both experimental and control owls ranged from 0–1575 m. Owls from experimentally depredated nests that dispersed did so within 8.4 ± 4.5 d (range: 0–25 d) following experimental egg removal.

NESTING BEHAVIOR

Burrowing owls were able to renest quickly and frequently following experimental nest predation, producing a large number of eggs during the breeding season. The average time between egg removal and clutch completion for six renesting attempts for which we knew the clutch completion date for the pair's subsequent clutch was 21 ± 3 d, indicating that owls renested quickly following nest predation. The owls showed an ability to produce several clutches within a breeding season regardless of dispersal: one pair produced three clutches in the same nest burrow, while another pair produced four clutches in four separate nest burrows, each separated by 203, 262 and 107 m, respectively. Of the eight females from experimental nests, three (38%) were known to renest at least once, three (38%) died in <28 d, and we were unable to determine if two (25%) renested. There was a decreasing trend in the number of eggs produced in each attempt. The average number of eggs for first, second, third and fourth clutches were seven (range 5–10, n = 8), six (range 3–9, n = 3), five

(range 4–6, n = 2) and four (n = 1), respectively. The three female owls from experimental nests that produced multiple clutches laid a total of 8, 19 and 29 eggs during two, three and four nesting attempts, respectively. Renesting was not limited to experimental owls; one pair of control owls successfully fledged at least one nestling and attempted a second clutch that failed. In addition, of the four female owls from control nests that failed during their first known nesting attempt, two died, causing the initial failure, but the two remaining owls successfully renested, one in the same burrow and the other 1575 m distant.

DISCUSSION

We hypothesized that the incidence and distance of dispersal would increase with nest predation. Our data was consistent with the hypothesis that nest predation increases the probability of dispersal. Haas (1998) reported similar results for between-season breeding dispersal, finding that both American robins (*Turdus migratorius*) and brown thrashers (*Toxostoma rufum*) were more likely to return to the same nest site following a successful nesting attempt the previous year than following experimental nest failure. Moreover, our results agree with other studies that found an association between nesting success and dispersal in burrowing owls, both within a breeding season (Rosier *et al.*, 2006) and between breeding seasons (Lutz and Plumpton, 1999; Catlin *et al.*, 2005).

Dispersal following nest predation could reduce the probability of losing a second clutch to predation (Powell and Frasch, 2000). The most frequent nest predator for burrowing owls in the agricultural area was the striped skunk, which often followed the linear waterways, depredating most nests along a section of road (Catlin, 2004). Coulombe (1971) also found that skunks depredated burrowing owl nests in the Imperial Valley, suggesting that skunks are common nest predators in some years. In this case, a burrowing owl could potentially avoid further nest predation by dispersing from the immediate area prior to renesting. We were unable to test for differences in dispersal distances between experimental and control owls because only one control owl dispersed. There was a great deal of variation in dispersal distance for owls whose nests were depredated, demonstrating that predation does not consistently affect dispersal distance, which may be due to a lack of benefit from longer distance dispersal in terms of nest predator avoidance (Greig-Smith, 1982; Powell and Frasch, 2000). It is also possible that this population has evolved under less predation pressure than others, which might have affected our results. The indication, however, from the year of the study was that predation can be heavy in some years, and this could have been the case in the past as well. Additionally, since this population uses both natural and artificial burrows, it is possible that the reactions of owls might differ between the two types of burrow, but there does not appear to be differences in occupancy or reproductive success related to the type of burrow (D. K. Rosenberg, pers. obs.), and all of the birds in the study were initially in artificial burrows so any bias should have been common among them.

Our examination of nesting behavior following nest predation demonstrated that owls in our population may attempt to breed several times during the breeding season following nest failure. The ability to attempt multiple nests and to produce many eggs may explain the variable response in dispersal to nest predation. If an owl can attempt several clutches in a given breeding season, then dispersing following nest predation may not be necessary to increase fitness. The control owls that renested following abandonment suggest that renesting was a strategy to deal with nest failure in general and not nest predation in particular. Despite the possibility of diminished returns, renesting has been shown to increase lifetime productivity in other avian species (Martin *et al.*, 1989; Hipfner, 2001), which could explain the renesting behavior that we observed. All but one of the renesting attempts that we

described followed the loss of eggs; it is possible that owls were more likely to renest following early stage losses because relatively minor effort was put forth. For instance, Slagsvold (1984) found that great tits (*Parus major*) had lower reproductive success following the experimental removal of a large brood than following the loss of a smaller brood, indicating that level of prior effort is an important determinant of renesting success. Renesting following initial failure has been observed among small raptors (Newton, 1979), and the large numbers of eggs produced by a single female owl in a season suggests that the cost of producing an average size clutch is not limiting. There was, however, a decreasing effort in each subsequent attempt, that could reflect diminished returns (or a net loss in productivity associated with larger clutches) from renesting attempts later in the breeding season (Kershner *et al.*, 2001), an accumulation of the costs of producing eggs, or possibly a direct reduction in response to nest predation (Doligez and Clobert, 2003). As further evidence of diminished returns, production of second broods is rare in western burrowing owls (Gervais and Rosenberg, 1999), suggesting that the energy demands and resource availability act to limit burrowing owl breeding later in the season. Our results highlight the variable behavioral responses to nest predation. Moreover, it appears that burrowing owls in the Imperial Valley may have adapted to nest predation both by dispersal and by an ability to produce several clutches within a single season.

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