BENEFITS OF SUPPLEMENTAL FEEDING ARE CLIMATE DEPENDENT IN THE SAN CLEMENTE LOGGERHEAD SHRIKE

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Abstract—Supplemental feeding is a key component to many conservation efforts. Because the effect of feeding on a target population's breeding biology interacts with weather in complex ways, supplemental feeding programs may be more influential on target populations in some years than in others. We examined the effect of supplemental feeding on breeding characteristics of San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*) during both relatively dry and wet years. From 2001 through 2007, the mean number of independent young produced by supplementally fed shrike pairs was 30% higher than for non-supplementally fed pairs. Shrike breeding phenology was affected by both rainfall and supplemental feeding, with the beneficial effects of supplemental feeding most evident in dry years. In dry years, supplementally fed pairs initiated breeding an average of 12 days earlier, were nearly a third again as likely to renest after successfully fledging young, and attempted a third again as many nests as non-fed pairs. None of these effects were observed following relatively wet winters. Supplemental feeding did not affect nest success, nor did it result in a statistically significant increase in independent young production regardless of winter rainfall. These observations indicate that supplemental feeding reduces the negative impacts of food limitation imposed by periodic drought, but does not mitigate predation pressure on nesting shrikes. Our study suggests that supplemental feeding efforts should vary from year to year based on winter rainfall, with greater efforts put forth in drought years than during relatively wet years. This study demonstrates that evaluating the effects of provisioning on breeding components can provide a sensitive indicator of whether or not a program is working and that understanding the proximate mechanisms through which supplemental feeding acts is an important step to optimizing adaptive management of endangered species.

INTRODUCTION

Release programs that place captive-reared birds into the wild have been an essential technique in the recovery of several endangered species (Nesbitt and Carpenter 1993; White et al. 2005). Food supplementation to help newly released individuals adjust to their environment is a component of many soft release programs (Castro et al. 2003; Kreger et al. 2005). In addition, supplemental food provisioning can augment reproductive output of wild-born individuals, and is thought to buffer populations from the threat of extinction due to environmental stochasticity (Kuehler et al. 2000; Schoech et al. 2007).

Because food limitation can have negative effects on population growth, supplementation can be an effective management tool when nutritional resources are limiting. This is most evident during the energy-intensive breeding season (Martin 1987). For example, reduction of arthropod populations during a drought year curtailed reproduction in four resident bird species inhabiting coastal sage scrub in southern California (Bolger et al. 2005). On the Channel Islands, the San Clemente sage sparrow (*Amphispiza belli clementeae*) exhibited reduced reproductive effort in drought years (Kaiser et al. 2008) when plant productivity was greatly reduced (Beaudry et al. 2004). Drought-driven changes in resource abundance can impose strong selection pressure on birds (Grant and Grant 1995; Van Noordwijk et al. 1995; Visser et al. 1998).

Food supplementation has been associated with greater reproductive output through a variety of mechanisms, including earlier egg laying, increased

clutch size, egg volume, increased nesting attempts and nest success, and reduced intervals between clutches (Martin 1987; Robb et al. 2008). The effect of supplemental feeding on reproductive output may interact with variation in weather patterns and predation pressure in complex ways (Schultz 1991; Zanette et al. 2006; Preston and Rotenberry 2006). Consequently, proper implementation and evaluation of a supplemental feeding program depend on understanding the mechanism(s) through which feeding affects reproductive output.

In this paper, we examine the effects of supplemental feeding on the breeding characteristics of the San Clemente loggerhead shrike (*Lanius ludovicianus mearnsi*; SCLS). Endemic to San Clemente Island, California, the wild population of this endangered subspecies declined to 14 individuals by 1988, likely due to habitat degradation and exacerbated predation by non-native species (Scott and Morrison 1990; Mader et al. 2000). Since then, the U.S. Navy established a multifaceted recovery program including intensive monitoring of wild birds, control of non-native predators, habitat restoration, captive breeding, population augmentation with captive-bred birds, and supplemental feeding of captive-bred birds in the wild. The wild shrike population has increased substantially since 2000. This recovery has been fueled, in part, by high reproductive rates; shrike pairs in the wild have averaged > 2.5 fledglings per pair per year from 2000 through 2007 (Bradley et al. 2007). Reproductive rates have been greater in relatively wet years, and bolstered in dry years by breeding season supplemental feeding in combination with rat (*Rattus rattus*) control (Heath et al. 2008).

The mechanisms through which supplemental feeding affects shrike fecundity, however, remain poorly understood. In particular, optimal allocation of future feeding efforts depends on whether supplemental feeding acts through mechanisms that mitigate predation pressure or mechanisms that mitigate resource limitation. If supplemental feeding helps to mitigate predation pressure, by increasing nest survival or reducing the time it takes for a pair to renest after nest failure, future efforts might be better aimed at feeding pairs that do not receive predator protection. If supplemental feeding mitigates resource limitation, by promoting earlier nesting, more nesting attempts per season, or

increasing renesting after successful attempts, future efforts might be best applied during drought years when resources are most limiting. Here we attempt to identify the mechanism or mechanisms though which supplemental feeding affects shrike fecundity. Because shrike reproduction is known to vary with rainfall (Heath et al. 2008), we also examine the data set for potential interactions between feeding, reproduction, and pre-breeding season precipitation. Although interactions between predation pressure and supplemental feeding may be as important as interactions between supplemental feeding and rainfall (Zanette et al. 2006; Preston and Rotenberry 2006), we do not examine these because supplemental feeding was associated with predator protection at sites and because we do not have accurate indices of predation pressure.

Study Species

SCLS are year-round residents of San Clemente Island, California. They are socially monogamous, and both male and female participate in nest building and in feeding and caring for young. Adults begin reproducing in their first year and have, on average, two broods per breeding season (Bent 1950). If initial nests fail, they can renest multiple times within the same breeding season (Yosef 1996). The breeding season begins with the forming of pairs at breeding territories, typically in February or March, and ends when the last broods fledge and young reach independence, typically in June and July (Bradley et al. 2007). Breeding territories are usually located in canyons where trees and shrubs provide nesting cover. Shrikes nest in a wide variety of plants and artificial substrates, but most nests are placed in island cherry (*Prunus lyonii*) or lemonade berry (*Rhus intergrifolia*) trees (Bradley et al. 2007).

Study Site

San Clemente Island lies 92 km west of the southern California coast. It is 148 km^2, making it the fourth largest of the Channel Islands. It has an arid climate, with a mean annual rainfall of 13 cm. Rainfall varies strongly both within and between years. Most precipitation falls between October and March. Because most rain falls over winter, spanning calendar years, bio-year accumulation (July–June) is more informative than annual

(January–December) rainfall in capturing relevant annual variation. Bio-year accumulation ranged from 3.8 to 40.9 cm between 2001 and 2007 (CS Northridge San Clemente Island Monitoring Project 2009). Plant phenology is closely tied to winter rainfall, with many plants failing to leaf out or flower in dry years (Beaudry et al. 2003, 2004). Drought years are also correlated with lower indices of rodent abundance on the island (Biteman et al. 2009).

The west side of the island has gentle sloping marine terraces covered in coastal scrub, and is cut by deep canyons that support a variety of tree and shrub species. The main plateau is dominated by grasslands with a regenerating cover of coyote brush (*Baccaharis salicifolia*). The eastern slope is steep, rugged, and covered with a mixture of grasses, coastal scrub, trees, and shrubs. Common tree and shrub species include oak (*Quercus tomentella*, and *Q. chrysolepsis*), island cherry and ironwood (*Lyonothamnus floribundus*), lemonade berry, toyon (*Heteromeles arbutifolia*), and sage (*Artimisia* sp.).

METHODS

We examined the effect of supplemental feeding on SCLS reproduction by comparing breeding characteristics between pairs that were supplementally provisioned prior to and during the breeding season and pairs that were not fed prior to or during the breeding season. Most supplementally fed birds were captive-bred and subsequently released onto SCI. The Institute for Wildlife Studies has carried out releases since 1999, using a variety of soft release techniques (Garcelon and Sharpe 1998; Fidorra et al. 2008). Generally, releases were carried out by transporting birds as single adults, paired adults, or in juvenile flocks to a release site where, depending on their breeding status, they were held in aviaries for several days to two months. Supplemental food was then provided at release sites through the remainder of the breeding season.

After release, adults and fledglings were fed at the site twice a day for the first three days, once a day for the next two weeks, then every other day until October when they were weaned to a 10-day feeding interval to encourage self-foraging (Fidorra et al. 2008). If birds remained at the release sites

beyond the first breeding season, they were fed once every 10 days year-round unless they had nestlings in a nest, at which point they were fed once every three to five days. On occasion, wild-born birds formally mated to released birds still living near release sites were provisioned in the same manner. Consequently, both provisioned and non-provisioned sites were utilized by wild-born, captive-born, and mixed-origin pairs.

Food was delivered to shrikes in one of two ways. At sites easily accessible from the central plateau, food was placed in a shaded dispenser raised 1.5–2 m off the ground on a metal post (Fig. 1a). At sites located in less accessible canyon bottoms, food was placed in a plastic tub, which was
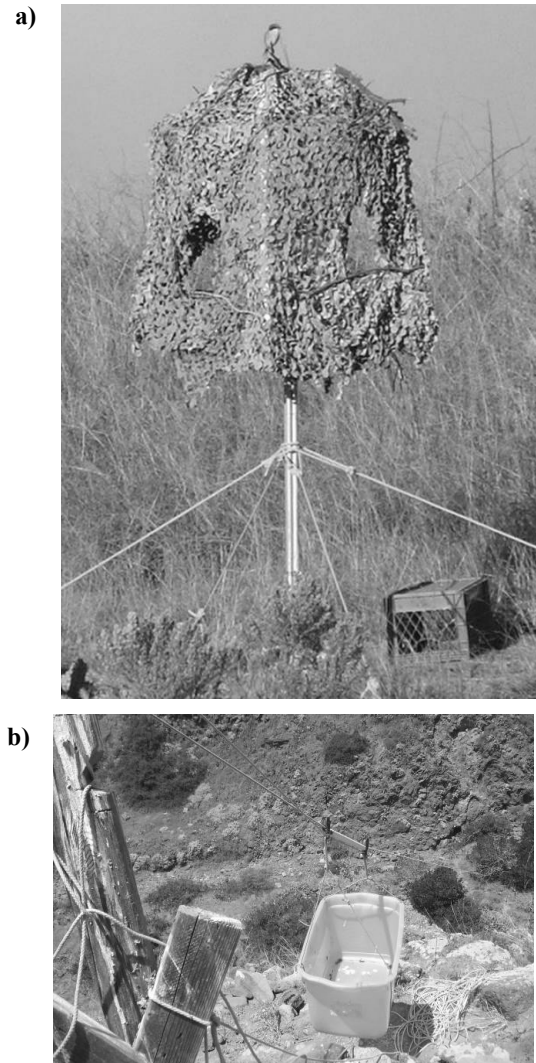
Figure 1. Photographs of supplemental feeding devices a) above canyon rims and b) for canyon bottom territories (photos courtesy A.-M. Easley).

delivered to the SCLS via a zip-line and pulley system (Fig. 1b). Once delivered, feeding behaviors were observed for 30 min and the numbers of food items eaten, fed to mates or nestlings, or cached were recorded. Food provided included live mice (*Mus musculus*), mealworms (*Tenebrio molitor*), and crickets (*Acheta domestica*). The amount that each shrike received was equivalent to 25–75 crickets and 25–75 mealworms, plus one to three mice per shrike per visit. When a pair had nestlings, the amount of crickets and mealworms provided was increased based on the number of nestlings in the nest. Live mice remaining after the observation period were removed so as not to attract shrike predators or competitors such as feral cats (*Felis catus*), kestrels (*Falco sparverius*), or common ravens (*Corvus corax*).

Breeding data were collected by biologists from Point Reyes Bird Observatory Conservation and the Institute for Wildlife Studies for every known SCLS pair on SCI from 1997 through 2007. During the non-breeding season, all known active and historic shrike territories were visited every 2–8 weeks, depending on accessibility. During the breeding season, territories were visited at least once a week, depending on nesting stage. During most visits, behavioral observations were made through spotting scopes from a distance of at least 100 m from nesting sites. Observation locations were chosen so that observers could see adult behaviors at or near the nest without disturbing the birds. Breeding status was inferred from observed behaviors (Scott and Morrison 1990). A nest was included in our sample if egg-laying behavior was observed. After hatching behavior was observed, nests were visited twice; once to count and age nestlings, and a second time to band nestlings when they were 9–11 days old. Birds were banded with United States Fish and Wildlife Service bands and a unique combination of three color bands. The vast majority of shrikes in the population could be uniquely identified by their color-band combinations.

Statistical Analyses

We compared estimates of reproductive parameters in wet years and in dry years between pairs that received supplemental food and those that did not, and examined interactions between feeding and rainfall. Specifically, we asked if supplemental feeding affected nest success (the probability that nests containing at least one egg subsequently produced at least one independent young), the onset of breeding (the date when a pair's first nest was initiated), renesting interval (the number of days between nest failure and egg hatching in the next nest attempt), and probability of attempting multiple clutches (the probability that a pair attempted an additional clutch after fledging young from their previous nest attempt).

We combined pairs from 2001 through 2007 for models comparing supplemental feeding. We excluded from our analysis sites that had the same pair of adults as the previous year ($n = 25$) to avoid the possibility that inter-annual mate fidelity might confound indices of reproductive success.

We used ANOVA (proc GLM SAS 8.0 SAS Institute Cary, NC) to analyze effects of feeding treatment and rainfall on clutch initiation date, time between nest attempts, and number of independent young. For each analysis, we nested feeding treatment within year and year within rainfall category. To check for interactions between weather and supplemental feeding and still account for the nested structure, we analyzed the difference between the value for each response variable at a site and the mean value for that variable for that year (hereafter, "annual residuals") and analyzed the effects of rainfall, supplemental feeding, and their interaction with an ANOVA. If the interaction term was significant at the 0.10 level, we subsequently compared feeding treatments separately for wet and dry years.

Because renesting probability, the number of nest attempts, and nest success could take on only a small number of values, they should be evaluated using logistic regression rather than ANOVA. However, preliminary analyses revealed that the nested structure used above made the results of logistic regression analysis difficult to interpret. To simplify interpretation, we conducted separate analyses for the effect of provisioning in wet and dry years on the annual residuals of these variables, which have a more continuous distribution. We applied an arcsine transformation to annual residuals of the two probabilities before analysis (Sokal and Rohlf 1995).

We did not use the standard Mayfield (Mayfield 1961) index to analyze nest success because our intensive monitoring throughout the year resulted in
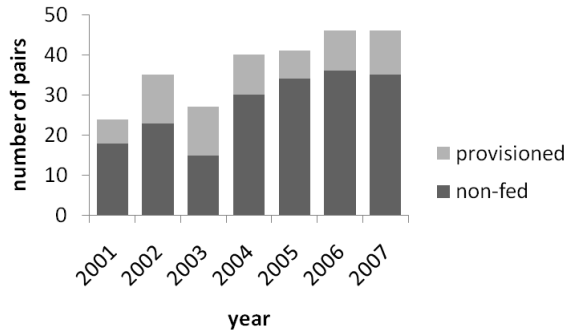
Figure 2. Number of breeding shrike pairs on San Clemente Island 2001–2007. Each bar represents the number of provisioned (light) and non-fed (dark) pairs known to have attempted at least one nest that year.

a very low chance that we failed to find nests before they failed. Before conducting analyses we reviewed data for normality and observed no significant deviations except as noted above.

The number and proportion of pairs that were supplementally fed varied year to year (Fig. 2). Wet years were defined as those with at least 100 mm rainfall during the winter months prior to the breeding season (November to February), and dry years as those with less than 100 mm rain in the same period. This cutoff point was chosen based on the large difference in breeding behaviors observed in another San Clemente endemic, the San Clemente sage sparrow, above and below the 100 mm winter rainfall threshold. We categorized 2001, 2003, and 2005 as wet years with 177 mm, 111mm, and 167 mm of annual rainfall respectively; and 2002, 2004, 2006, and 2007 as dry years with annual precipitation ranging from 34 to 40 mm.

For each comparison, we included breeding pairs comprised of individuals that had been in the wild for at least one winter. We excluded same-sex pairs, pairs for which egg-laying was never confirmed, and pairs where one or both individuals had been released from captivity that breeding year. To account for varying degrees of predator control effort from site to site (Cooper et al. 2005), only pairs that nested at breeding territories protected by both rodent poisoning and trapping were considered in analyses of reproductive success. Furthermore, we excluded nests from analyses of first clutch initiation date or post-failure renesting interval if the timing of visits to the breeding site did not allow us to confirm the date of egg-laying or nest failure to

Table 1. Sample sizes used to analyze the effects of supplemental feeding on breeding components in relatively wet and dry years.

Breeding component	Provisioned		Not provisioned	
	Wet	Dry	Wet	Dry
Clutch initiation	19	23	45	86
Post success renesting probability	15	19	39	53
Number of nesting attempts	22	27	53	96
Post failure renesting interval	6	10	19	19
Nest success	22	27	53	96
Independent juvenile protection	22	27	53	96

within five days of accuracy. Sample sizes for each of the treatment groups can be found in Table 1.

RESULTS

Birds began nest building as early as January 17, and there was significant annual variation in the start of the breeding season, which was not related to winter rainfall (Fig. 3; Table 2). Within years,
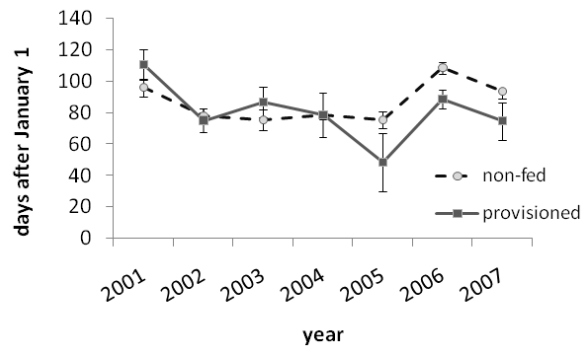

Figure 3. Annual variation in breeding dates. The average day of the year that pairs initiated nest building of their first nest attempt and whether or not they were provisioned from 2005–2007. Error bars represent +/- 1 standard error.

Table 2. Results from nested ANOVA analyses.

Response variable	Rainfall		Year		Provisioning	
	F	p	F	p	F	p
Clutch initiation	0.31	0.578	7.56	<0.001	2.11	0.046
Post failure renesting interval	0.31	0.581	1.11	0.368	0.78	0.605
Independent juvenile production	3.76	0.054	2.61	0.026	0.45	0.869

provisioned pairs tended to start nest building before unfed pairs, especially in the latter half of the study (Fig. 3; Table 2). There was a rainfall by provisioning interaction ($F_{1,169}$=3.35, p=0.07) such that provisioned pairs began nesting an average of 12 days earlier than non-fed pairs during dry years ($F_{1,107}$=4.88, p=0.03), while provisioning did not affect clutch initiation during wet years ($F_{1,62}$=0.37, p=0.55). A post-hoc comparison between earlier (2001–2004) and later (2005–2007) years of the study did indicate a significant interaction between time-period and effect of provisioning on breeding season initiation date ($F_{1,169}$=11.68, p<0.001), with a significantly positive (i.e., earlier initiation) effect in the latter ($F_{1,83}$=12.12, p<0.001) but not earlier ($F_{1,86}$=1.43, p=0.24) periods.

The average time between nest failure and hatching date of the following nest attempt was 27.25 (+/- 1.75 sem) days. Neither supplemental feeding nor rainfall impacted the amount of time pairs needed to renest following nest failure (Table 2), nor was there a significant rainfall by feeding interaction ($F_{1,50}$=1.15, p=0.221).

Whether or not a pair renested after successfully fledging young was positively influenced by supplemental feeding in dry but not wet years (Fig. 4a, dry years: $F_{1,70}$=5.35, p=0.023; wet years: $F_{1,52}$=0.20, p=0.658). In the absence of provisioning, shrikes were only 37% as likely to renest after fledging young in dry years as they were in wet years. In contrast, provisioned birds were nearly equally likely to renest regardless of rainfall. As a consequence, provisioned birds attempted a third again as many nests as non-fed pairs in dry years (Fig. 4b, dry years: $F_{1,121}$=9.94, p=0.002; wet years: $F_{1,73}$=0.31, p=0.581).

Nest success averaged 54% among predator protected sites and did not differ significantly between wet and dry years or between provisioned and non-fed pairs (Fig. 5, weather: $F_{1,126}$=0.11, p=0.746; supplemental feeding $F_{1,126}$=0.20,

p=0.6334; weather x feeding interaction: $F_{1,126}$=0.16, p=0.687).

There were more independent young produced in wet than in dry years (Fig. 6; Table 2). Although there was a trend toward greater production of young at provisioned sites, the difference was not statistically significant (Table 2) and there was no rainfall by feeding interaction ($F_{1,194}$=0.02, p=0.891).
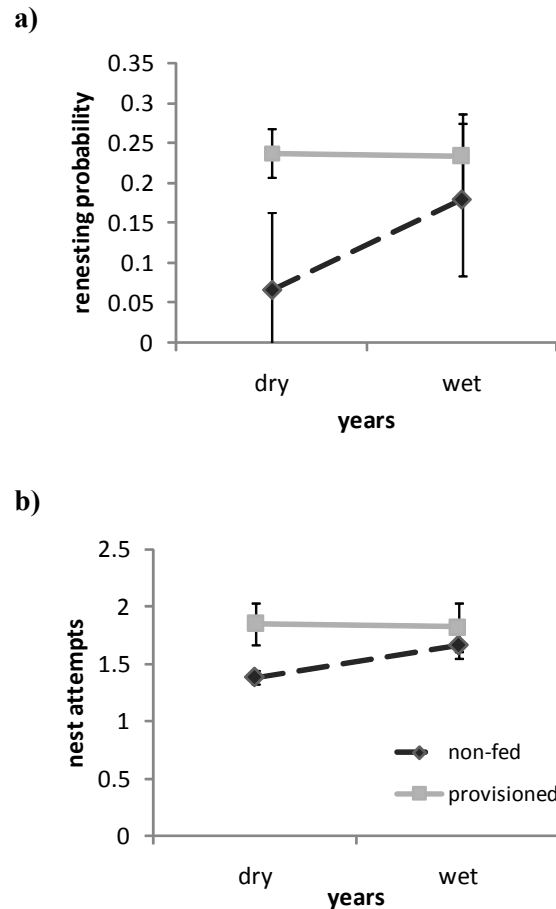
a)

b)

Figure 4. Effect of supplemental feeding on nest attempts. Supplemental feeding increases both a) the probability of renesting after successful nest attempt and b) the total number of nest attempts in a breeding season during dry but not wet years. Error bars represent +/- 1 standard error.
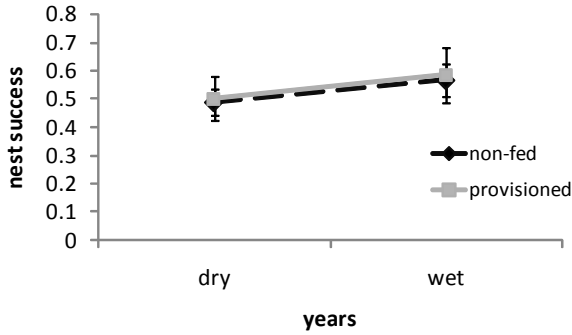
Figure 5. The probability that a nest produces at least one independent young did not differ between wet and dry years or between provisioned and non-fed pairs. Error bars represent +/- 1 standard error.

DISCUSSION

Provisioning promoted earlier breeding and increased the chance that pairs produced multiple clutches. These effects were most apparent during relatively dry years, and weak or nonexistent during relatively wet years. We did not find evidence that supplemental feeding affected either nest failure rates or the interval between nest failure and subsequent renesting attempts. These results suggest that supplemental feeding reduced the impacts of resource limitation but not the impacts of nest predation.

These results corroborate research that food can be limiting to reproductive success in temperate regions (Martin 1987), despite contrary arguments suggesting that birds can adapt to food scarcity (Ettinger and King 1980; King and Murphy 1985),
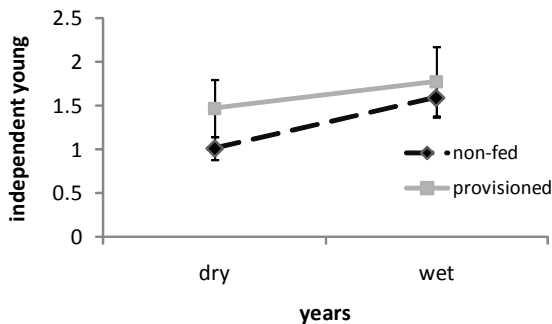

Figure 6. Number of independent young produced. The number of independent young produced per breeding shrike pair was not significantly different between wet and dry years or between provisioned and non-fed pairs. Error bars represent +/- 1 standard error.

or that the energy requirements of birds are less than environmental resource availability (Rotenberry 1980; Rosenberg et al. 1982). We found evidence that food limits both the timing of clutch initiation and numbers of clutches a pair can attempt in a season. Similar results by Aparicio and Bonal (2002) found a relationship between body condition and commencement of breeding. Earlier clutch initiation is often advantageous because it enables the production of offspring at a time of year when food is more abundant, resulting in increased fledgling survival (Korpimaki and Wiehn 1998; Preston et al. 2006; but see Verboven et al. 2001). Earlier clutch initiation also leads to increased fecundity by promoting increased breeding attempts (Nol and Smith 1987).

Even for early breeders with a sufficiently long breeding season, the production of multiple broods depends on a bird's energy reserves (Martin 1987). For example, in great tits (*Parus major*) double brooding was influenced not by how early first nests were complete but by the abundance of caterpillars after the first clutch was completed (Verboven et al. 2001). Consequently, supplemental feeding may increase the number of nest attempts (Nagy and Holmes 2005; Zanette et al. 2006) by providing quality energy resources late into the breeding season. Although the number of clutches produced during a breeding season greatly influences overall production (Morrison and Bolger 2002; Nagy and Holmes 2005), this is one of only a few studies that have examined whether supplemental feeding increases the probability of multiple brooding or numbers of nesting attempts (Verboven et al. 2001; Zanette et al. 2006), and fewer have demonstrated an effect (Zanette et al. 2006).

In the California Channel Islands and Gulf of California islands both primary productivity (Beaudry et al. 2003, 2004) and small herbivore abundance (Polis et al. 1997) are closely tied to rainfall. In relatively wet years, resources are abundant as insects respond quickly to winter plant flushes after winter rains, and rodenticide consumption at protected sites indicate that rodent populations respond within a few months (Biteman et al. 2009). In contrast, during dry years many plants fail to even leaf out (Beaudry et al. 2003), insect populations crash (Polis et al. 1997), and rodents are scarce (Biteman et al. 2009). This annual variation in natural resources corresponded with the

observed interaction between rainfall and supplemental feeding. The lack of effect of supplemental feeding on the components of breeding associated with resource limitation is consistent with a "saturation effect," whereby provisioning only benefits a population when resources are relatively low (Schulz 1991). The saturation effect we observed associated with relatively wet years suggests that resources are not limiting shrike reproductive effort except during drought years. It further implies that provisioning wild birds is most beneficial during dry years, and will have little impact on the population during relatively wet ones.

As it is currently implemented, supplemental feeding does not influence those aspects of breeding impacted by predators. Supplemental feeding has been demonstrated to increase the protection of nestlings and fledglings in other species (Martin 1992) by increasing the amount of time available to adults for anti-predator behavior (Rastogi et al. 2006). An increase in nest attendance by provisioned adults (Arcese and Smith 1988; Wiebe and Bortolotti 1994; Dewey and Kennedy 2001; Nagy and Holmes 2004) has been shown to reduce overall nest predation (Yom-Tov 1974; Hogstedt 1981). Supplemental feeding may indeed benefit shrike nests in this way but go undetected because of the association of supplemental feeding and predator protection at shrike nesting sites. For example, lower predation pressure associated with predator protection might reduce the influence of supplemental feeding on predator-mediated breeding traits (i.e., nest success, post-failure renest interval) in the same way higher resource abundance reduced the effect on associated traits (e.g., clutch initiation date, probability of producing multiple clutches, and number of nest attempts). If so, our study design, imposed by the shrike recovery program, would likely miss any influence of supplemental feeding on predator-mediated breeding variables. However, the only previous experimental manipulations controlling both feeding and predation pressure suggest that supplemental feeding acts independently (Preston and Rotenberry 2006) or synergistically (Zanette et al. 2006) with reduced predator control; a saturating effect of predator control on the potential benefits of supplemental feeding has not yet been published.

Like Heath et al. (2008), we did not find a statistically significant effect of provisioning on independent young production, though there is a non-significant trend of greater production among provisioned compared to non-fed pairs. It should be noted that we used the same data as Heath et al. (2008) with the addition of nests from 2007. Part of the reason we did not detect a significant effect may be that we did not simultaneously control for the relatively large impact of other variables influencing production (Heath et al. 2008) such as whether the adult female was wild or captive born (wild females produced more young) and male age (older males produced more young). Since parent age and female origin were well mixed among treatments, they were unlikely to bias our results, but do introduce sources of variability in independent young production that reduce our power to detect the effects of provisioning. Another contributing factor may be that even though provisioned pairs attempt more nests in a breeding season, nest success was lower with each subsequent nest attempt (Institute for Wildlife Studies, unpublished data).

Using the effects of provisioning on breeding components to evaluate the efficacy of supplemental feeding programs has two advantages. First, because there is a more direct link between the two, the breeding components will be a more sensitive indicator than young production of whether or not a program is working. Second, understanding the mechanism(s) through which supplemental feeding acts is an important step to optimizing conservation efforts through adaptive management. For example, our study suggests that supplemental feeding efforts should vary from year to year based on winter rainfall, with greater efforts put forth in drought years; while resources may be better devoted to other programs (e.g., greater nest protection) during relatively wet years.

ACKNOWLEDGMENTS

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