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Rodent control and food supplementation increase productivity of endangered San Clemente Loggerhead Shrikes (*Lanius ludovicianus mearnsi*)

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ABSTRACT

Habitat loss and predation by exotic predators have contributed to the decline of many island populations of birds, including San Clemente Loggerhead Shrikes (*Lanius ludovicianus mearnsi*). This critically endangered subspecies has been the recipient of an extensive and expensive recovery effort, including a captive breeding and release program. We examined the effects of life-history characteristics, rainfall, and management, particularly food supplementation and rat (*Rattus rattus*) control, on the breeding productivity of 172 San Clemente Loggerhead Shrike pairs from 2000 to 2006. Annual fecundity and the number of fledglings reaching independence per pair varied with year and were closely correlated with prebreeding (November–March) precipitation levels. Annual fecundity increased as a result of management implemented between April and July each year. Shrike pairs receiving no management during this period produced a mean of 1.9 fledglings. Pairs receiving both food and rat control produced an average of 2.5 more fledglings than pairs receiving no management, while pairs receiving rat control alone produced an average of 1.1 more fledglings than pairs receiving no management during this period. Wild-origin females produced an average of 0.8 more fledglings per pair than captive-origin females, while older males produced an average of 0.9 more fledglings and independent young relative to inexperienced males. The effects of food supplementation and rat control on San Clemente Loggerhead Shrikes were most pronounced during dry years, suggesting such management should be emphasized when prebreeding precipitation levels are below historical averages. These techniques offer an effective means to increase breeding productivity of avian species in immediate threat of extinction.

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1. Introduction

The San Clemente Loggerhead Shrike (*Lanius ludovicianus mearnsi*) is a critically endangered (United States Fish and Wildlife Service, 1977) subspecies of songbird endemic to San Clemente Island, California, USA. Population estimates ranged between 5 and 11 breeding pairs from 1985 to 1988 (Scott and Morrison, 1990). The historical decline of the population is attributed to habitat loss caused by exotic herbivores coupled with predation by native and exotic predators (Scott and Morrison, 1990), mirroring factors resulting in the decline of many bird populations (Robbins et al., 1989; Côte and Sutherland, 1997). An extensive management program was initiated in 1992 to recover the San Clemente Loggerhead Shrike population, which included a captive propagation program, soft-releases, food supplementation, predator management including feral cat and rat control, herbivore removal, and native plant restoration (Morrison et al., 1995). As a result, the population of San Clemente Loggerhead Shrikes in the wild has increased dramatically since 1999 (Heath et al., 2007), and the population was estimated at 50 breeding pairs in the wild in 2006 (Bradley et al., 2007). Given the immense resources (approximately US\$1.7 million annually) and effort that have gone into the recovery program, it is imperative to determine which management techniques have contributed to increasing population growth in order to better direct conservation efforts in the future for this and other critically endangered avian populations.

Nest predation is a major cause of nest failure for avian populations (O'Connor, 1991; Martin, 1993), including Loggerhead Shrikes (Walk et al., 2006). Over 75% of the world's islands are inhabited by exotic rodents (Brockie et al., 1988), and rats have been identified as a major cause of nest mortality for many avian species, especially on islands (Atkinson, 1977, 1985; Diamond, 1985; Tweed et al., 2006). Predator management, including rat control, can increase survival and/or breeding productivity of avian populations (Côte and Sutherland, 1997; Innes et al., 1999; VanderWerf and Smith, 2002; Moorhouse et al., 2003; Armstrong et al., 2006). Because nest depredation typically results in the loss of all nest contents, reduced predation can increase annual fecundity through the production of multiple broods (Martin, 1992; Morrison and Bolger, 2002).

Food limitation can also have negative effects on populations, which should be most apparent during the energy-demanding breeding season (Castro et al., 2003). Unlike nest predation, food availability affects annual fecundity primarily through incremental changes in clutch size, hatchability, and nestling survival (Rodenhouse and Holmes, 1992; Newton, 1998; Zanette et al., 2006b). Food supplementation is a technique commonly employed in avian research and to aid in the recovery of endangered bird populations. Food supplementation has been demonstrated to increase clutch size (Castro et al., 2003; Arcese and Smith, 1988; Nagy and Holmes, 2005; Schoech et al., 2008; Zanette et al., 2006b), nestling weight (Dewey and Kennedy, 2001; Garcia et al., 1993); fledgling production (Castro et al., 2003; Verhulst, 1994; Hochachka and Boag, 1987; Hogstedt, 1981), independent young production (Arcese and Smith, 1988; Simons and Martin, 1990), number of breeding attempts (Arcese and Smith, 1988; Nagy and

Holmes, 2005; Preston and Rotenberry, 2006a; Schoech et al., 2008) and to advance laying date (Hogstedt, 1981; Schoech, 1996; Aparicio and Bonal, 2002).

The effects of increased food availability and predation on breeding productivity often vary with annual rainfall (Morrison and Bolger, 2002; Preston and Rotenberry, 2006a; Zanette et al., 2006a). In arid ecosystems, precipitation and temperature affect seasonal patterns in primary productivity (Gibbs and Grant, 1987; Polis et al., 1997) and insect populations (Bolger et al., 2000). In such systems, a positive relationship between rainfall and annual fecundity has been well documented (Gibbs and Grant, 1987; Rotenberry and Wiens, 1991; Bolger et al., 2005), which is attributed to both the increased availability of resources required for nesting as well as alterations in predator activity (Morrison and Bolger, 2002). Here we examine whether territory-specific rat control and food supplementation affect breeding productivity of San Clemente Loggerhead Shrikes and evaluate the effects of life-history traits. Because San Clemente Island experiences substantial variation in annual precipitation, we hypothesize the benefits of food supplementation and rat control will be greatest in years with low rainfall.

2. Study bird and study area

San Clemente Loggerhead Shrikes are primarily monogamous, and both members participate in nest building and chick feeding (Morrison et al., 1995). Females are the sole incubators, and males provision females on the nest. The breeding phenology of this subspecies was described by Scott and Morrison (1990). Pair formation begins in January, and first clutch completion typically occurs from late February to March. Egg-laying takes 4–6 days with one egg laid per day to clutch completion. Clutch size typically ranges from four to six and incubation lasts 16–18 days. Fledging typically occurs 16–20 days following hatch and parents feed fledglings frequently until dispersal. Scott and Morrison (1990) reported that parental care extended an average of 50 days following hatch, but juveniles typically begin foraging by age 35 days. Loggerhead Shrikes are “double brooded” and will persistently re-nest after nest failure as well as after a successful brood. All nesting behaviors typically cease by July. Loggerhead Shrikes are highly territorial (Yosef, 1996) and birds on San Clemente Island exhibited minimum home range sizes (based on at least 30 recorded locations) of approximately 16 ha (Lynn et al., 2006). San Clemente Loggerhead Shrikes feed primarily on lizards (53%), mice (28%), insects (15%), and birds (4%) (Scott and Morrison, 1995). A captive release program was instituted to aid in the recovery of the population and 294 Shrikes were released on San Clemente Island between 1999 and 2006 (Heath et al., 2007). We employed soft-release techniques, whereby Shrikes were placed in aviaries constructed near suitable habitat and allowed a period of acclimatization ranging from a few days to several weeks prior to being released.

San Clemente Island (32°50'N, 118°30'W) is the southernmost of the eight Channel Islands, CA, USA. The island is 38 km long, 2.4 to 6.4 km wide, and has an area of 146 km². The island's highest point is 599 m in elevation. The eastern side of San Clemente Island drops steeply into the Pacific

Ocean while the western side gradually descends through a series of marine terraces to the shoreline. Numerous canyons transect both the eastern and western portions of the island. Introduced sheep (*Ovis aries*), goats (*Capris hircus*), and pigs (*Sus scrofa*) substantially reduced native vegetation, primarily from 1936 to 1976 (Scott and Morrison, 1990). The last introduced herbivore was removed in the early 1990s (Morrison et al., 1995) and a native plant restoration program is facilitating the recovery of the island's flora (US Navy, 2002). Three recently introduced mammals, black rat (*Rattus rattus*), house mouse (*Mus musculus*), and feral cat (*Felis catus*) persist on the island, as well as native predators including the island fox (*Urocyon littoralis*) and numerous bird species. The dominant plant communities consist of native and non-native grasses and desert maritime scrub. The majority of woody vegetation types, which include *Rhus intergrifolia*, *Lyonothamnus floribundus*, *Prunus lyonii*, *Quercus tomentella*, *Quercus chrysolepis*, and *Heteromeles arbutifolia*, are located within the canyons and constitute the primary Loggerhead Shrike habitat on the island. San Clemente Island is owned and administered by the US Navy and portions of the island are used for military training, including shore bombardment ranges. Data from this study were collected from December 2000 to July 2006.

3. Methods

3.1. Climatic conditions

We compared San Clemente prebreeding season precipitation for each year from 2000 to 2006 with the prebreeding season precipitation on Catalina Island, averaged from 1949 to 2006, in order to determine "above-average" rainfall years and "below-average" years on San Clemente Island. Rainfall data has been collected on San Clemente Island since 1996, but has been collected since 1949 at a weather station on Catalina Island (Catalina Conservancy, 2007), approximately 45 km northeast of the San Clemente Island weather station. Rainfall records for San Clemente Island from 2000 and 2006 were provided by California State University, Northridge. A regression analysis done between the annual prebreeding season rainfall totals at both stations over the period 1996–2006 yielded an r^2 value of 0.96. Because >80% of rainfall for this region falls between November and March (Preston and Rotenberry, 2006a), we defined the rainfall over this five-month interval as "prebreeding season precipitation" (Morrison and Bolger, 2002).

3.2. Monitoring

We attempted to locate and identify all Shrikes in the wild (wild-born and captive-born), map minimum home ranges, and describe breeding phenology for each pair. Each breeding pair was visited one to two times per week and the length of each observation period varied as needed to determine the presence and breeding status of pairs and to read color-band combinations. Observers used spotting scopes from a vantage point at least 50 m from the nest site. Egg-laying, incubation, hatching, and nestling stages were inferred for each pair by observing diagnostic stage-specific breeding activities and

behaviors. To reduce the likelihood of nest disturbance and predation risks, we minimized the number of visits to each nest. Nest contents were assessed using a mirrored pole once following hatch to determine the appropriate date to band nestlings. We attempted to color-band nestlings at approximately 10 days-of-age; the majority of the population is color-banded for individual recognition. Fledging was confirmed when we heard begging calls by fledglings and observed parents delivering food to areas away from the nest. We recorded the total number of offspring that fledged from each nest. Fledglings that reached 40 days of age (based on estimated hatch date) were considered "independent." The number of fledglings and individuals reaching independence are minimum estimates and do not include young that may have died soon after fledging or that moved a substantial distance from natal sites prior to independence, respectively. To minimize underestimation resulting from undetected fledglings, we increased the frequency of nest monitoring at each territory when chicks were approaching fledgling age (based on known hatch dates and chick age estimates). A nest was identified as "failed" when either adult was confirmed attending a new nest site or the female stopped exhibiting incubation behaviors prior to the anticipated hatch date. Nests were inspected to ascertain the cause of failure where possible. Time-lapse video cameras were also used on a small number of nests to determine nest fate.

3.3. Rat control

Rodent control was conducted at individual breeding territories using Quintox[®], a commercially manufactured rodenticide containing cholecalciferol (Vitamin D₃). Cholecalciferol is a subacute rodenticide that mobilizes calcium stores from bones to bloodstream resulting in hypercalcemia and calcification of the blood vessels (Buckle, 1994). Quintox[®] generally requires the ingestion of multiple doses to cause death, with a LD₅₀ of 8.72 g/rat and 1.13 g/mouse (Donlan et al., 2003). Quintox[®] was selected to minimize secondary effects to other sensitive species such as the native island fox (*Urocyon littoralis*). Rodenticide bait stations were placed within 50 m of a nest, or within the core of an individual or pair's territory prior to nesting. Rodenticide was placed at ground level in tamper-proof boxes and the number of stations deployed varied based on the habitat heterogeneity of each territory, as rat density in arid ecosystems has been shown to be correlated with an index of vegetation biomass (Clark, 1980). Stations were weighed monthly to determine consumption levels and refilled. Stations were not refilled monthly if it was determined that the activity would potentially disturb nesting Shrikes or if weather or US Navy training prevented access into canyons.

We used live-capture box traps (Tomahawk model 102, Tomahawk Live Trap Company, Tomahawk, Wisconsin) to capture rats at a subset of territories receiving rodenticide during the period from December to March each year. Live traps were implemented in an attempt to capture rats that did not enter rodenticide bait stations or when rodenticide was unavailable. Traps were placed throughout the canyon bottoms of Shrike territories and checked daily. The number of traps deployed and the number of nights the traps were opened varied from site to site based on accessibility. When

Shrike pairs formed we ceased live-trapping to minimize disturbance during breeding. Box traps had a cage mesh design, which allowed mice to escape through the wire mesh. Traps that had bait missing (presumably consumed by mice) were excluded from totals.

3.4. Supplementary feeding

We offered supplemental food in the form of live crickets (*Acheta domestica*), mealworms (*Tenebrio molitor*), and mice (*Mus musculus*). Food was offered in translucent plastic tubs (62.4 l, Rubbermaid®) that were either placed on the ground within a breeding territory or lowered into canyons using a rope and pulley system. The latter method did not require observers to enter canyons and thus minimized disturbance. Diets varied according to the number of Shrikes on-site and their breeding stage; we typically offered 25 crickets, 25 mealworms, and one mouse for each Shrike on site, including nestlings and fledglings. We conducted 30 min of observations during each feeding event to identify Shrikes taking food. Food was offered at each site a minimum of every 10 days, but we attempted to offer food more frequently (every 2–5 days) at territories reaching the nestling and fledgling stages. Beginning in 2002, we also offered supplemental food at some sites using an automated feeder system designed to gradually dispense mealworms between observer visits. We stocked 1000 (± 100) mealworms in dispensers every 10 days. We directly observed at least one member of a pair taking food at 100% of territories receiving supplementation. Total biomass of food provided was calculated by assuming an approximate mass for each cricket (0.19 g), mealworm (0.07 g), and mouse (12.5 g). While we assumed the majority of food offered was taken by Shrikes, some food went unused or was taken by non-target species.

The number of Shrike pairs offered supplemental food was dependent on site accessibility as well as each individual's origin (captive-born or wild). Captive-origin Shrikes were fed using plastic tubs while in captivity and associate the tubs with food. As only captive-origin Shrikes or wild-origin individuals that were "taught" this behavior by their captive-origin mate would enter the supplemental feeding tubs, we could only provide supplemental food to pairs with at least one captive-origin member, or to a Shrike whose natal site had food supplementation. All sites receiving food supplementation also received rat control because we assumed pairs acclimated to receiving food were tolerant of the presence of researchers and less likely to abandon a site. We selected territories to receive predator control and/or food supplementation opportunistically in order to maximize the number of pairs that could be managed based on staff and resource availability.

3.5. Statistical analyses

Each Shrike pair was assigned to one of three management categories for two 4-month periods: December–March and April–July. The management categories were (1) no management, (2) rat control, and (3) rat control and food supplementation. We considered a site "rat controlled" if any of the following treatments were applied over a four month period: (a) at least 250 g of rodenticide deployed along with 50 traps

set, (b) 500 g of rodenticide alone, or (c) 100 traps alone. We considered pairs that received a minimum of 300 g of food as "food supplemented" during a period.

We used a General Linear Model in Systat (Version 9, SPSS Inc.) to determine the effects of six categorical variables on breeding productivity of each Shrike pair per year: (1) December–March management, (2) April–July management, (3) male origin (captive or wild), (4) female origin (captive or wild), (5) pair history (new pair or previously bred together) and (6) year. The dependent variables used were annual fecundity and number of independent young produced per pair per year. We defined annual fecundity as the number of fledglings produced by a pair in a breeding season. We performed two additional analyses using a General Linear Model with the above variables as well as "female age" (second-year or after-second-year) and "male age" (second-year or after-second-year) for the subset of pairs where this variable was known. We used polynomial regression to compare annual fecundity and number of independent young per pair with prebreeding precipitation. To further investigate the effects of management during the period of April–July, we compared annual fecundity and independent young production during "above-average" rainfall years versus "below-average" years using Analysis of Variance (ANOVA).

Data used in this study does not include all breeding pairs on San Clemente Island over the study period. We excluded pairs from analyses when we could not definitely determine their breeding status or accurately assess fledgling output. Only pairs that attempted to nest (e.g., egg-laying) were included. Sites at which additional management occurred (i.e., cross-fostering; eggs or nestlings brought into captivity) were excluded. Pairs with nest cameras were included if they did not cause abandonment. Shrikes breeding during the same year in which they were released were also excluded to account for potential naiveté associated with recent captivity (Banks et al., 2002; Biggins et al., 1999). We reviewed the residuals of general linear models for normality and homoscedasticity and observed no significant deviations.

4. Results

4.1. Rainfall

Prebreeding rainfall levels varied on San Clemente Island during the six-year study period (Fig. 1), and averaged 12.3 cm during the six years. Prebreeding precipitation on Catalina Island averaged 11.0 cm from 1949 to 2006. Prebreeding rainfall levels on San Clemente Island were higher than the Catalina Island average in 2001, 2003, and 2005 and below the Catalina Island average in 2002, 2004, and 2006 (Fig. 1).

4.2. Nest monitoring

We monitored the breeding phenology of 172 breeding pairs that were included in analyses: 20 pairs in 2001, 34 pairs in 2002, 19 pairs in 2003, 35 pairs in 2004, 32 pairs in 2005, and 32 pairs in 2006. We confirmed the age of the male for 152 pairs, and the age of the female for 145 pairs. Six pairs failed to reach the nesting (egg-laying) stage and were excluded from analyses. Three of these pairs received supplemental

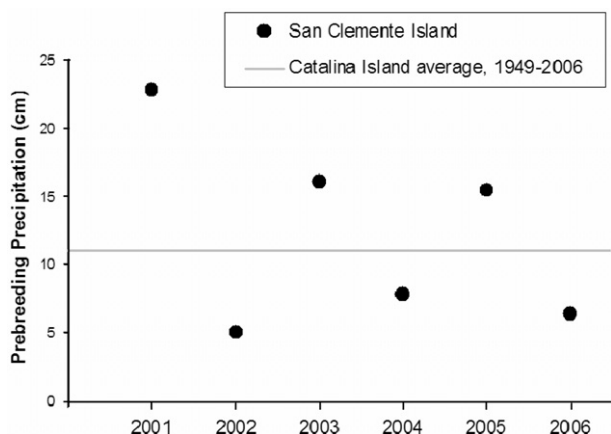


Fig. 1 – Annual prebreeding precipitation on San Clemente Island, 2000–2006. Pre-breeding precipitation is defined as that falling from November to March. Gray line is prebreeding precipitation average for Catalina Island from 1949 to 2006.

food and rat control and three of the pairs received no management.

4.3. Rat management

The mean amount of rodenticide applied at individual territories between December of the previous year and July was 4.1 kg (20% consumed; $n = 16$ territories) in 2001, 5.2 kg (27% consumed; $n = 25$) in 2002, 4.8 kg (8% consumed; $n = 15$) in 2003, 5.3 kg (28% consumed; $n = 18$) in 2004, 4.5 kg (22% consumed; $n = 18$) in 2005, and 6.2 kg (42% consumed; $n = 18$) in 2006 (Fig. 2). We could not quantify rodenticide taken by rats versus mice. Large rainfall events during January and February in both 2001 and 2005 washed away bait stations at several territories, resulting in low rodenticide application during those periods (Fig. 2). Rodenticide was not applied from December 2001 to February 2002 while the product was unavailable.

The number of territories trapped, the number of available traps, and capture rate varied by year (Table 1). In 2002, more trapping was performed to compensate for the lack of rodenticide application during December 2001 through February 2002.

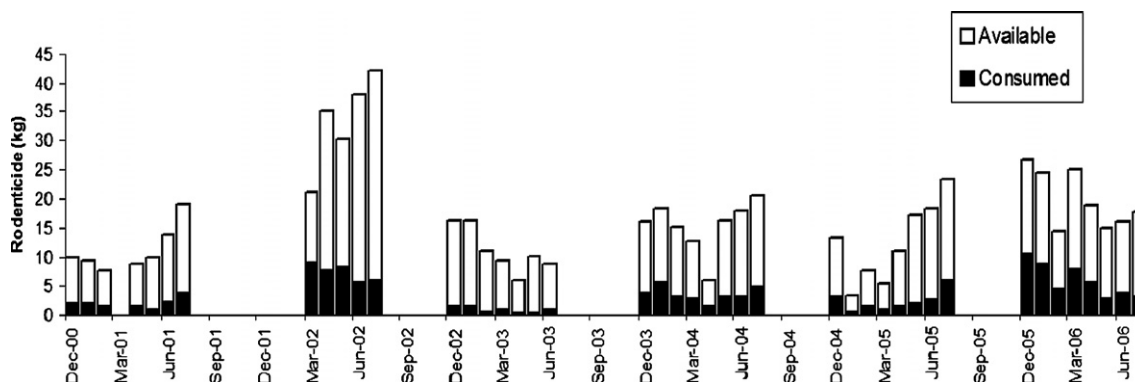


Fig. 2 – Available and consumed rodenticide (kg) at Shrike territories from December 2000 to July 2006. The number of territories receiving rodenticide treatment varied by year: $n = 16$ (2001); $n = 25$ (2002); $n = 15$ (2003); $n = 18$ (2004); $n = 18$ (2005); and 18 (2006).

Capture rates were higher in 2002 (13%) and 2006 (18%) relative to other years (range 0.2–3%). During the six-year study period, capture rate averaged 7.2% and 331 rats were removed.

4.4. Food supplementation

The mean biomass of food offered at each breeding territory between December and July was 1.7 kg ($n = 8$) in 2001, 2.3 kg ($n = 16$) in 2002, 3.3 kg ($n = 9$) in 2003, 3.1 kg ($n = 10$) in 2004, 2.7 kg ($n = 4$) in 2005, and 3.5 kg ($n = 8$) in 2006 (Fig. 3).

4.5. Breeding productivity

Annual fecundity ($p = 0.009$) and the number of fledglings reaching independence per pair ($p = 0.004$) varied with year (Table 2). Annual fecundity was affected by management category during April–July ($p = 0.02$); pairs receiving both food and rat control produced an average of 2.5 more fledglings than pairs receiving no management while pairs receiving rat control alone produced an average of 1.1 more fledglings than pairs receiving no management (Table 2). Female origin ($p = 0.04$) affected annual fecundity and wild-origin females produced an average of 0.8 more fledglings per pair than cap-

Table 1 – The number of sites trapped for rats on San Clements Island between December and March, including number of rats removed

Year	No. territories trapped	No. available traps ^a	No. rats removed	Capture rate ^b
2000–2001	7	442	10	0.02
2001–2002	22	1625	204	0.13
2002–2003	11	998	2	0.00
2003–2004	8	564	8	0.01
2004–2005	8	457	13	0.03
2005–2006	10	524	94	0.18
Total	66	4610	331	0.07

^a Available traps is defined as the total number of traps that were available for capture summed over the number of nights that traps were opened.

^b Capture rate is the number of rats removed divided by the number of available traps.

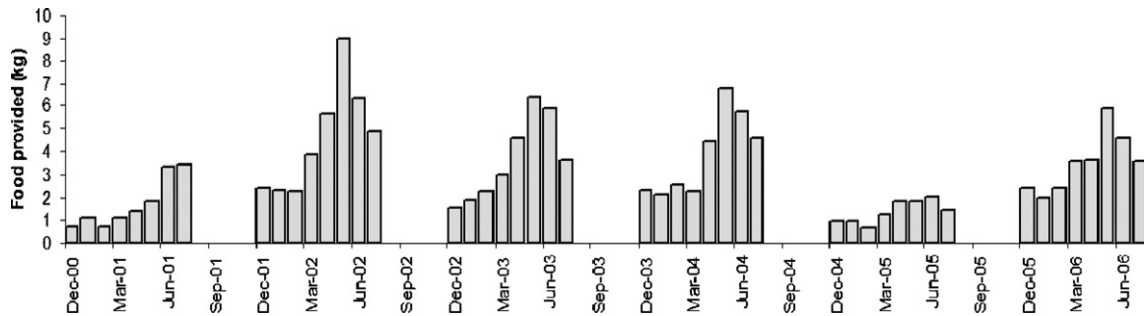


Fig. 3 – Total supplemental food (kg) provided at Shrike territories from December 2000 to July 2006. Food consisted of mealworms, crickets and mice. The number of territories supplemented varied by year: $n = 8$ (2001); $n = 16$ (2002); $n = 9$ (2003); $n = 10$ (2004); $n = 4$ (2005); and $n = 8$ (2006). All territories receiving food supplementation received rat control.

Table 2 – Results of general linear models of the effect of male origin, pair experience, year, and management category during two periods, December to March and April to July, on annual fecundity (No. fledglings per pair) and number of independent young per pair ($N = 172$)

Factor	n	Annual Fecundity		No. Independent young per pair	
		Mean (S.E.)	F-ratio (p)	Mean (S.E.)	F-ratio (p)
Male origin					
Captive	54	2.64 (0.39)	3.12	1.90 (0.32)	2.75
Wild	118	3.55 (0.28)	(0.08)	2.62 (0.24)	(0.10)
Female origin					
Captive	65	2.69 (0.28)	4.45	1.92 (0.24)	4.69
Wild	107	3.50 (0.30)	(0.04)	2.61 (0.25)	(0.03)
Pair experience					
New pair	131	2.72 (0.23)	3.55	2.01 (0.19)	2.31
Pre-existing pair	41	3.47 (0.35)	(0.06)	2.52 (0.30)	(0.13)
Dec–Mar					
No management	80	3.23 (0.43)	0.71	1.97 (0.36)	1.13
Rat control	50	2.70 (0.41)	(0.49)	1.97 (0.34)	(0.33)
Rat control + food	42	3.36 (0.58)		2.86 (0.48)	
Apr–Jul					
No management	62	1.89 (0.55)	4.13	1.49 (0.46)	2.30
Rat control	55	2.98 (0.42)	(0.02)	2.26 (0.35)	(0.10)
Rat control + food	55	4.41 (0.48)		3.04 (0.40)	
Year					
2001	20	3.43 (0.54)	3.17	2.27 (0.45)	3.59
2002	34	2.38 (0.39)	(0.009)	1.75 (0.33)	(0.004)
2003	19	3.99 (0.51)		3.07 (0.43)	
2004	35	3.04 (0.38)		2.43 (0.32)	
2005	32	3.61 (0.42)		2.73 (0.35)	
2006	32	2.13 (0.39)		1.34 (0.33)	

tive-origin females. Pair experience ($p = 0.06$), male origin ($p = 0.08$), and management during the period from December to March ($p = 0.49$) did not significantly affect annual fecundity (Table 2). Number of fledglings reaching independence per pair was affected by female origin ($p = 0.03$); wild-origin females produced an average of 0.7 more independent fledglings than captive-origin females. Male origin ($p = 0.10$), pair experience ($p = 0.13$), and management during December to

March ($p = 0.33$) or April to July ($p = 0.10$) did not affect the production of independent young.

Male age affected both annual fecundity ($F_{1,138} = 4.60$; $p = 0.03$) and independent young production ($F_{1,138} = 5.81$; $p = 0.02$). After-second-year males produced an average of 0.9 more fledglings and independent young compared to second-year (inexperienced) males. Female age did not affect

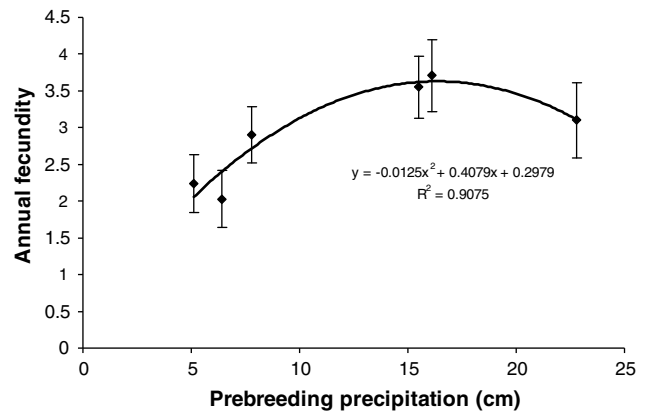


Fig. 4 – Polynomial regression of annual fecundity of San Clemente Loggerhead Shrikes as a function of prebreeding precipitation. Bars represent standard error.

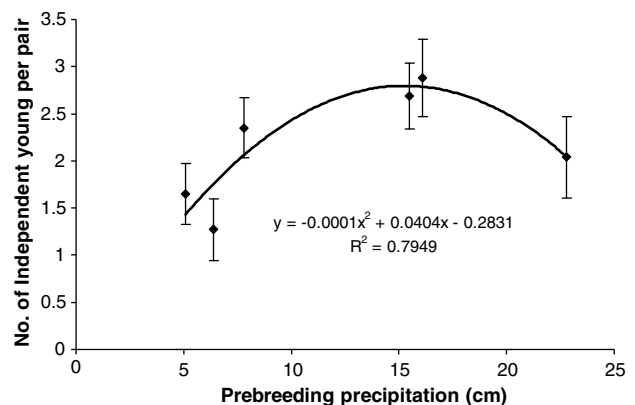


Fig. 5 – Polynomial regression of the number of independent young per pair of San Clemente Loggerhead Shrikes as a function of prebreeding precipitation. Bars represent standard error.

annual fecundity ($F_{1,131} = 0.18$; $p = 0.67$) or independent young production ($F_{1,131} = 1.64$; $p = 0.20$).

Because “year” was significant in all analyses, we examined the effect of rainfall on breeding productivity using nonlinear regression with quadratic equations. Annual fecundity ($r^2 = 0.91$, Fig. 4) and number of fledglings reaching independence per pair ($r^2 = 0.79$, Fig. 5) peaked at intermediate prebreeding precipitation levels, with lower values in very low and very high rainfall years. April to July management affected annual fecundity during “below-average” dry years ($F_{2,98} = 7.67$; $p = 0.001$) but not during “above-average” wet years ($F_{2,68} = 2.67$; $p = 0.077$). During dry years, pairs receiving rat control and food supplementation produced an average of 1.8 more

fledglings than pairs receiving no management (Fig. 6). April–July management affected independent young production during dry years ($F_{2,98} = 11.23$; $p < 0.001$) but not during wet years ($F_{2,68} = 2.06$; $p = 0.14$). During dry years, pairs receiving rat control and food supplementation produced an average of 1.8 more independent young per pair than pairs receiving no control, while pairs receiving rat control produced an average of 1.1 more independent young than pairs receiving no control (Fig. 7).

5. Discussion

Our results show that annual fecundity and independent young production of San Clemente Loggerhead Shrikes were affected by a variety of factors. The six years of this study encompassed substantial variation in annual rainfall including one of the driest years (2002) recorded for this arid region (Bolger et al., 2005). Thus it was not surprising that we observed such strong variability in annual offspring production. Differences in prebreeding precipitation appeared to account for the majority of these annual effects, although we lack data on annual changes in predator abundance that may also have contributed. Breeding productivity declined at both high and low levels of prebreeding precipitation, most likely as a result of low prey availability (low rainfall) and increased chick mortality due to weather and predation (high rainfall). However, this conclusion is based largely on the results of one high rainfall year and merits further investigation.

Management of the population had the greatest effect during the period from April to July, which coincides with the primary nestling and fledgling periods of this species. We anecdotally observed adults taking higher quantities of supplemental food during these stages and delivering them directly to offspring. Management effects were most evident in dry years, when pairs receiving both rat control and food supplementation from April to July produced twice as many fledglings and nearly three times as many independent young as pairs receiving no management. A positive relationship between rainfall and annual fecundity in avian populations has been well documented in arid ecosystems (Rotenberry and Wiens, 1991; Bolger et al., 2005) and is attributed largely to increased food abundance, including insects (Bolger et al., 2000). Food supplementation likely offset low food availability during dry years and reduced the likelihood of nestling and fledgling starvation. Predator control may also be more important during dry years as predators may become more dependent on the eggs and young of birds when alternate food resources are limited (hypothesized in Rotenberry and Wiens, 1991). Management from December to March had no effect on productivity suggesting that supplemental food availability during the egg-laying period did not increase brood size. While management activity from December to March did not produce significant effects on annual fecundity, it remains unclear if sites receiving food supplementation catalyzed the formation of breeding pairs, allowed adults to choose better breeding partners, or prolonged adult survival (Garcia et al., 1993; Wiebe and Bortolotti, 1994).

Food availability and predation may have interactive effects on breeding productivity and should not be considered independently (Zanette et al., 2006a). Food supplementation has been demonstrated to increase nest/brood attendance

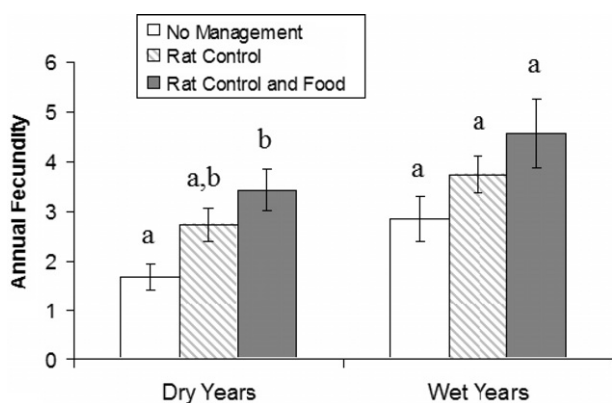


Fig. 6 – Annual fecundity of San Clemente Loggerhead Shrikes under three levels of management during the period of April through July for below-average (i.e., dry) precipitation years (2002, 2004, 2006) and above-average (i.e., wet) precipitation years (2001, 2003, 2005). Bars represent standard error. Treatments sharing the same letter were not significantly different from one another ($P > 0.05$).

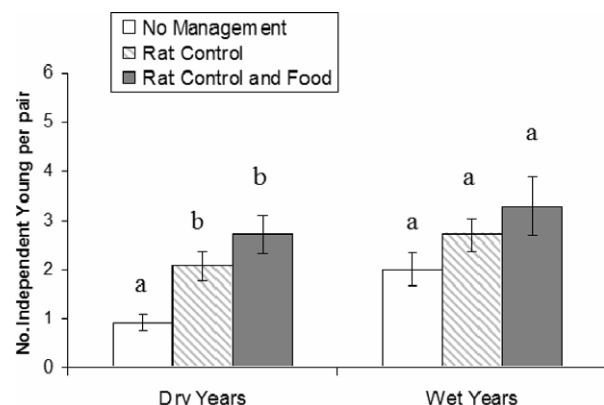


Fig. 7 – The number of independent young per pair per year of San Clemente Loggerhead Shrikes under three levels of management during the period of April through July for below-average (i.e., dry) precipitation years (2002, 2004, 2006) and above-average (i.e., wet) precipitation years (2001, 2003, 2005). Bars represent standard error. Treatments sharing the same letter were not significantly different from one another ($P > 0.05$).

by adults (Dewey and Kennedy, 2001; Wiebe and Bortolotti, 1994; Arcese and Smith, 1988; Nagy and Holmes, 2005), thus increasing the amount of time available for anti-predator behavior (Rastogi et al., 2006) and reducing nest predation (Yom-Tov, 1974; Hogstedt, 1981). Zanette et al. (2003, 2006a) showed food availability and predators interact to affect both nest predation and partial clutch or brood loss. Song Sparrows (*Melospiza melodia*) in a “low predator” treatment that received food supplementation fledged 1.8 times more young than expected if the effects of food and predators were independent and additive (Zanette et al., 2006a). However, Preston and Rotenberry (2006b) did not observe synergistic effects with nest predation for Wrentits (*Chamaea fasciata*) in an arid ecosystem and emphasized that such effects would be largely dependent on the life-history of the species and the environment in which they live. We were unable to determine if synergistic effects were present in Shrikes because we did not offer any pairs food supplementation without rat control. In addition to rat removal, rodenticide application may result in the localized reduction of Shrike prey (mice) within territories, thereby increasing the importance of simultaneous food supplementation. We recommend adding food-supplementation-only treatments for some Shrike pairs to determine if such synergistic effects are present.

Captive-origin females and second-year (inexperienced) males produced fewer offspring than older, wild-origin San Clemente Loggerhead Shrikes. Second-year birds typically achieve lower reproductive success than older birds (Curio, 1983; Skutch, 1976), even in environments where food is abundant (Skagen, 1988). The fact that male age was significant and female age was not in affecting fledgling and independent young production has been observed in other species (VanderWerf, 2004) and likely relates to the male's role as primary food provider for young (Scott and Morrison, 1990). We were not surprised that captive-origin individuals performed poorer than wild-origin individuals. While reintroduced individuals often exhibit naïve behaviors that increase their short term vulnerability to predators after release (Banks et al., 2002; Biggins et al., 1999), naïvete may also affect critical decisions influencing breeding productivity, including nest site selection, nest construction, nest attendance, and food-provisioning behaviors. Pair experience may be influential in determining breeding success in San Clemente Loggerhead Shrikes, as pairs that have previously bred together, besides being older, may mate together again only if the previous effort produced offspring.

Rat control resulted in greater offspring production, as has been observed in other avian populations (Innes et al., 1999; VanderWerf and Smith, 2002; Moorhouse et al., 2003; Armstrong et al., 2006). We were unable to determine the number of rats or mice removed using rodenticide or what proportion of nest predation is attributed to rats on San Clemente Island. Nest cameras captured rat predation at nests in 2004 and 2005, and evidence at partially predated nests in 2005 strongly implicated rats. We need to better understand the efficacy of localized rodenticide application on rat removal on San Clemente Island and estimate the proportion of nest predation attributable to different species. Scott and Morrison (1990) observed Common Ravens preying on three nests during the 1980s, and an unidentified mammal (cat or fox) was captured

by a nest camera depredating a Shrike nest in 2001. It is unclear if other predators on San Clemente Island shift their diets from rodents to birds in response to rodent removal (Murphy and Bradfield, 1992) or how quickly new predators fill the ecological niches vacated by rodent removal. Changing baits and toxins are possible techniques to combat behavioral and physiological resistance of rats to bait (Prakash, 1988), but we are limited in the types of rodenticide we can implement on San Clemente Island in order to minimize effects on other species of concern. The eradication of rats from islands is extremely difficult (Rodríguez et al., 2006), and predator reduction programs present no long-term solution to nest predation on San Clemente Island. The optimal strategy remains to maximize the efficacy of rat control to increase breeding productivity while natural and restorative processes gradually increase breeding habitat.

Predator management and food supplementation may result in population growth only when environmental conditions permit (Côte and Sutherland, 1997) and San Clemente Loggerhead Shrikes may be limited by resource availability during the non-breeding season (Cade and Woods, 1997; Temple, 1995). Factors affecting overwinter survival of San Clemente Loggerhead Shrikes need to be further researched to determine if increased productivity attributed to food supplementation and rat control is effectively leading to increased population growth, as in other restoration programs (Armstrong et al., 2007). Our management efforts may fail to increase population growth if surviving juveniles starve over the winter, perish from overwinter predation, or fail to establish a breeding territory in subsequent years.

Endangered species biologists often must utilize all the tools and resources at their disposal to recover populations from the brink of extinction. Our results demonstrate how food supplementation and rat control can increase breeding output of the San Clemente Loggerhead Shrike population and identify the most effective time of the year to provide specific management actions, namely during the nestling and fledgling periods from April to July. However, such management needs to be implemented with a solid understanding of species' ecology, and managers must closely consider life-history characteristics and the timing of management interventions to achieve desired effects. Additionally, factors out of the managers' control (e.g., climate) may play a large role in the success of the program. We found the effects of our management program were most pronounced during dry years and recommend that predator control and food supplementation on San Clemente Island should be emphasized when prebreeding precipitation levels are below historical averages. While labor intensive, predator control and food supplementation are effective options to increase breeding productivity of avian species under immediate threat of extinction. These techniques may buffer populations from extinction until other prerequisites of long-term species persistence, e.g. habitat restoration, are attained.

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