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# FOOD LIMITATION OF AVIAN REPRODUCTION: AN EXPERIMENT WITH THE CACTUS WREN[1]

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*Abstract.* Food limitation of reproduction during the nestling stage was tested by supplementing food only during this stage in Cactus Wrens. Parents offered supplemental food fed their young more (volume per unit time) than unsupplemented parents in 2 yr of experimentation. In 1986, food-supplemented nestlings had greater mass and linear measures, whereas in 1987, most food-supplemented nestlings had greater mass, but not linear dimensions, than their controls. In 1986, survivorship of young both in the nest and during 4-6 wk after fledging, was greater with food supplementation than without. In 1987, survivorship differences were not significant. Food supplementation enhanced annual reproduction of parents because more food-supplemented Cactus Wrens laid second clutches than controls in 1987, the only year when this was examined. We conclude that food availability during the nestling stage can limit present reproduction, enhance the likelihood of additional reproduction, or both, in Cactus Wrens.

*Key words: Cactus Wrens;* Campylorhynchus brunneicapillus; *experimental ecology; food limitation; food supplementation; nestling stage; population ecology; reproduction; reproductive ecology.*

## INTRODUCTION

Lack (1947) argued that clutch size in altricial birds is limited by the number of nestlings that parents can adequately feed. Efforts expended to meet the energy demands of nestlings may also affect future reproductive output of parents (Williams 1966, Charnov and Krebs 1974, see Martin 1987). Modified versions of Lack's hypothesis or other hypotheses have been advanced, which all assume that foraging requirements for nestlings are an important limit on present and future reproduction (Cody 1966, Williams 1966, Hogstedt 1980, Ricklefs 1980, Slagsvold 1982, 1984, Lundberg 1985, Martin 1987, but see Nur 1986). Yet, this commonly held assumption has not been adequately tested.

Experimental manipulations of brood size often show that offspring production decreases with increasing brood size in experimentally enlarged broods, suggesting that food is limiting at greater than normal brood sizes (for review see Martin 1987). However, these studies do not address whether offspring production of naturally sized broods would increase with greater food availability. Supplementation of food to unmanipulated broods provides a clearer test of whether food normally limits reproduction; parents should use additional food to increase survival chances of nestlings and improve their own future reproductive output if food availability normally limits such components.

Previous studies have not assessed food limitation during the nestling stage alone. For example, five studies in which supplemental food was provided did so during earlier stages (i.e., egg production, incubation) as well as the nestling stage (Yom-Tov 1974, von Bromssen and Jansson 1980, van Riper 1984, Davies and Lundberg 1985, Arcese and Smith 1988). Consequently, food limitation during the nestling period could not be separated from food limitation during earlier stages.

Two other studies (Crossner 1977, Hochachka and Boag 1987) provided supplemental food only during the nestling period, but each of these studies included other design complexities that masked interpretations. Hochachka and Boag (1987) compared 1 yr in which food was supplemented only during the nestling stage with two subsequent years in which food was supplemented during both the nestling period and earlier stages. Fledging success was greater in food-supplemented nests in the latter 2 yr only. Such results may indicate that food limitation did not exist during the nestling stage (i.e., earlier stages were more important) or that food limitation varies among years and was coincidentally less limiting in the year when food was added only during the nestling stage. Crossner (1977) provided the only clear evidence that food addition during the nestling stage can influence reproductive output. However, he manipulated brood size in addition to providing supplemental food. This manipulation obscured whether clutch size was normally at a level that could take advantage of additional food dur-

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ing nestling feeding. Moreover, he did not consider effects on future reproduction of adults. Only one food supplementation study examined effects on subsequent reproduction (von Bromssen and Jansson 1980). They found positive effects on one of two species examined, but again, food was supplied both before and during the nestling stage.

Here, we examine whether reproduction is limited by food availability during the nestling stage for the Cactus Wren (*Campylorhynchus brunneicapillus*). We supplemented food after eggs hatched until fledging in a natural population of Cactus Wrens during two breeding seasons. We also examined effects of added food on current and future reproductive output.

## METHODS

### *Study site and organism*

A 59-ha study site was established within the Usery Mountain Recreation Area of the Maricopa County Park system located near Phoenix, Arizona (township 2 north, range 7 east). The site was flagged in a 50-m grid on a south-facing, gradual slope, 600 m in elevation. The site supports typical Sonoran Desert vegetation including chainfruit cholla (*Opuntia fulgida*) and saguaro (*Carnegia giganteus*) cacti, bursage (*Ambrosia deltoidea*), and jojoba (*Simmondsia chinensis*) bushes, with palo verde (*Cercidium floridum* and *C. microphyllum*) and ironwood (*Olneya tesota*) trees in the abundant washes.

The Cactus Wren is a year-round resident of the Sonoran Desert and is territorial all year (Anderson and Anderson 1973). They lay their first eggs in late February or early March and breeding continues until June. Some Cactus Wrens lay and rear two broods during this period. Juveniles remain on parental territories until December or January, when they disperse.

Cactus Wrens prefer to nest in cholla cacti (*Opuntia* spp.) (McGee 1985). Nests may also occur in other thorny plants (Anderson and Anderson 1973). Nests are built with grasses and enclosed with a roof. Both parents feed the young, but only females incubate. Males perform most of the territorial defense though females will occasionally sing. Basic biology of the Cactus Wren is given by Anderson and Anderson (1973).

### *Food supplementation experiment*

The search for active nests began in January of both years. Nests were paired with another nest of the same or similar hatching date and the same number of hatchlings. The decision as to which nest in a pair was the experimental vs. control was based on a coin toss. This pairing technique controlled for effects of nest timing, brood size, and unpredictable weather changes on nest success.

Food supplementation began on the hatching date or 1 or 2 d thereafter, and food was supplied every other day for the entire nestling period (20 d). Supplies of supplemental food lasted at least 1, and often 2 d. Supplemental food consisted of laboratory-reared mealworms (*Tenebrio molitor*) and caterpillars (Family Noctuidae: *Pseudaletia* sp. and *Trichoplusia* sp.). Mealworms were chosen because they have been used in previous food supplementation experiments successfully. Caterpillars were added to provide a varied diet and because similar kinds of caterpillars are used by Cactus Wrens naturally. Mealworms were purchased commercially, and caterpillars were supplied by the Cotton Research Laboratory of the United States Department of Agriculture in Phoenix, Arizona. Approximately 300 mealworms and caterpillars (35 g) were placed in a double plastic bowl with the outer bowl filled with water. This design provided a moat that foraging ants could not cross and kept the larvae cool so they could live at least 2 d. The plastic bowls were lodged in cholla 1–2 m from the active nest. Parents usually found this food within 1 d. Other birds in the area (Curve-billed Thrasher, *Toxostoma curvirostre* and Gila Woodpecker, *Melanerpes uropygialis*) occasionally found the food bowls and used them, but Cactus Wrens had quicker access and used the majority of the food (L. Simons, *personal observation*).

### *Data collection and analysis*

To estimate rates of food delivery, we observed nests for 2-h periods beginning shortly after dawn. Food deliveries were sampled 28 times in each year, yielding 14 paired comparisons between food-supplemented and control nests per year. In 1986, rates of food delivery were sampled for two age classes (5–8 and 11–15 d old). Six pairs of nests were sampled during only one of the age classes, whereas four pairs were sampled at both age classes. In 1987, all but two nest pairs were sampled at older ages (12–15 d after hatching); the two pairs were sampled at 8 d of age. All nest pairs were sampled only once in 1987. Both nests in a pair were observed at the same age.

The number of food items carried in the parent's bill was noted for each trip to the nest. Length and width of each prey item was estimated in millimetre increments by comparison to the parent's bill and using a 20× telescope. Prey items ranged from 1 × 2 to 5 × 60 mm in size. The volume of each prey item was estimated as the volume of a cylinder ($\pi r^2 l$) where $r$ = ½ estimated width and $l$ = estimated length of the prey item. Food items were not seen clearly enough to estimate their size in 20.4% of trips to food-supplemented nests and 35.8% of trips to control nests. Consequently, trips lacking estimates of prey size were assigned the mean volume delivered during adequately observed trips in the same hour. Because prey items lacking estimates were likely to be smaller than the average item observed, substituting mean volume probably overestimates food delivery to nests. However, because more trips were estimated for control nests, this bias leads to a conservative test for the experimental effect. Total food volume delivered in the

2-h sample period was summed for each nest and compared between food-supplemented and control nests. The number and volume of supplemental food items, as a proportion of total food brought, was calculated on the basis of the adequately observed deliveries.

Nestlings were weighed and measured at 8 and 15 d of age, and color-banded at 15 d of age. Visits and measurements after 15 d of age were not possible because premature fledging can occur. Mass was measured to the nearest 0.1 g using a 30-g Pesola spring scale. Dial calipers were used to measure the following linear morphological measurements on nestlings: tarsus length, wing chord, and tail length.

Playback recordings were used in all nest areas to census survivorship of fledglings 4–6 wk after fledging in 1986 and 4 wk after fledging in 1987. Juvenile Cactus Wrens came to sing in response to these recordings with their parents at 4 wk of age and older. Individuals were identified by their color bands.

In 1987, all nest areas were searched for new nests 2 and 4 wk after fledging to assess renesting frequency. When new nests were found, they were watched until parents approached to attend the nest. Approximately 40% of parents had been mist-netted and color-banded earlier in the season, and were therefore readily identified. The others were identified by the associated fledglings that were color-banded. Therefore, the ownership of all new nests was known. Renesting attempts are unlikely to have been missed because Cactus Wrens remain in the same territory throughout the breeding season, and their nests are conspicuous and easy to find. The only incidence of remating occurred after the death of a female. She was replaced by a female that had been observed as a nestling the previous year. The older male retained his territory and began a new nest with the new female approximately 2 wk after the death of his former mate.

Wilcoxon signed-ranks tests for paired data were used for nearly all comparisons between food-supplemented and control nests (Pratt and Gibbons 1981). One-tailed tests were used because effects in only one direction are meaningful to the hypotheses tested. The *G* test for independence was used to test for dependence of renesting on food availability (Sokal and Rohlf 1981). The relationship between mass at fledging and survivorship was tested using one-way ANOVA after checking for normality (Sokal and Rohlf 1981). We used a median test (Sokal and Rohlf 1989) to test for differences in clutch size of new nests because the data were not normally distributed. Student's *t* tests were used for various other comparisons (see *Results*). To test if Cactus Wrens began breeding earlier in either year, each day of the breeding season was numbered starting at 1 on 25 February of each year. The number corresponding to the laying date of the first egg was assigned to each nest. We then used a *t* test on this assigned variable to compare laying dates between 1986 and 1987.

Maximum and minimum temperatures were read daily by personnel of the Maricopa Park and Recreation Department from a Taylor max-min thermometer located approximately 1 km north of the study site. The thermometer was in a ventilated styrofoam box with the north side open. These temperatures were compared to those taken at the Sky Harbor International Airport Weather Station located 20 km east of the study site in Phoenix, Arizona. Maximum temperatures taken near the study site were consistently 1°–2° C higher than Sky Harbor, while minimum temperatures were 1°–2° lower than Sky Harbor records. For the purpose of comparing climatic conditions between the 2 yr, Sky Harbor data reflects the same trends that were detected using the more local measurements. Since 30-yr averages exist for Sky Harbor data but not for the local climatological data, Sky Harbor data were used in the comparisons made in this study.

## RESULTS

### *Comparisons between years*

*Climatic differences between years.*—Fall and winter precipitation was greater preceding the 1986 season than the 1987 season (Table 1). Preceding the 1986 season, precipitation was greater than the 30-yr average in 4 out of 5 mo, whereas precipitation was less than the 30-yr average in 4 out of 5 mo preceding the 1987 season. Temperatures were higher than average in both 1986 and 1987, although the onset of high temperatures was earlier in 1986 than 1987 (Table 2); daily highs that were equal to or above 32° began earlier in 1986 than in 1987 (Table 2).

*Laying date and clutch size.*—Cactus Wrens began laying eggs slightly earlier in 1986 than 1987, but this difference was not significant (*t* test, $P > .05$, Table 3). Mean clutch size did not differ between the two breeding seasons ($\bar{X} \pm \text{SD} = 3.00 \pm 0.40$, $N = 62$ in 1986 and $3.05 \pm 0.48$, $N = 37$ in 1987). Clutch sizes other than three were infrequent (22% of nests had two or four eggs in 1986, 16% in 1987).

*Food delivery to control nests.*—Food items brought to control nests were compared between years. Grasshoppers were more abundant in nestling diets in 1987 than in 1986, while lepidopteran larvae were more abundant in 1986 than 1987 (Table 4). Rates of food delivery to control nests were marginally greater in 1987 ($\bar{X} \pm \text{SD} = 2.30 \pm 0.79$ $\text{cm}^3 \cdot \text{nestling}^{-1} \cdot \text{h}^{-1}$) than in 1986 ($1.76 \pm 0.75$ $\text{cm}^3 \cdot \text{nestling}^{-1} \cdot \text{h}^{-1}$) (*t* test, $P = .072$, df = 26).

*Mass and survivorship of young.*—Offspring from control nests were compared between years. Nestling masses at 15 d of age were significantly greater in 1987 than 1986 (*t* test, $P = .036$; for 1986 $\bar{X} \pm \text{SD} = 28.05 \pm 2.24$, $N = 33$; for 1987 $\bar{X} \pm \text{SD} = 29.89 \pm 4.38$, $N = 32$). Survival of young while in the nest was not significantly different between years (*G* test, $P > .05$, df = 1). However, survival for the first 4–6 wk after

TABLE 1. Precipitation during the fall and winter months preceding the 1986 and 1987 breeding seasons. Data are from Sky Harbor Airport monthly summaries. Numbers in parentheses are departures from the 30-yr average for each month.

| | Precipitation (cm) | | | | | |
|---|---|---|---|---|---|---|
| | Sep | Oct | Nov | Dec | Jan | Total |
| 1986 | 4.06<br>(+2.44) | 2.34<br>(+0.74) | 4.04<br>(+2.67) | 2.18<br>(+0.08) | 0.18<br>(−1.68) | 12.80<br>(+4.25) |
| 1987 | 1.19<br>(−0.43) | 1.04<br>(−0.56) | 0.08<br>(−1.30) | 3.51<br>(+1.40) | 1.70<br>(−0.15) | 7.52<br>(−1.04) |

fledging was significantly greater in 1987 (16/33) than 1986 (7/34) (*G* test, $P < .05$, df = 1).

*Relationship between mass at fledging and survivorship.*—Mass at 15 d of age was compared between fledglings that could be located 4–6 wk after fledging and those that were missing and presumed dead. Fledglings that survived 4–6 wk after fledging tended to be greater in mass than nonsurvivors in 1986 ($\bar{X} = 31.2$ vs. 29.6 g, respectively), but not in 1987 ($\bar{X} = 30.4$ and 30.3 g, respectively) (Table 5).

### *Food supplementation experiment*

*Food delivery to the nest.*—For 1986, two nestling age classes were tested separately for differences in food amount received between food-supplemented and control nests. Food-supplemented parents delivered more food to nestlings of both age groups in 1986 (Fig. 1). For 1987, all age classes were tested together. Food delivery rates were also greater in food-supplemented nests in 1987 (Fig. 1).

Supplemental food comprised 70.5% of the food items and 74.8% of the volume of food delivered to food-supplemented nests in 1986. In 1987, 84.8% of the food items and 79.7% of the food volume delivered to food-supplemented nests was supplemental food.

*Nestling growth.*—At 8 d of age, few significant differences existed between body masses of food-supplemented and control nestlings in either year (Fig. 2). However, by 15 d of age all mass measures, except the largest nestling mass in 1987 broods ($P = .068$), were greater in food-supplemented nests (Fig. 2); increases ranged from 3 to 14%. Differential mortality was responsible for the lack of statistical difference between the largest nestlings in 1987. In 1987, a control nest fledged only one nestling of four, while the paired experimental nest fledged all four. The remaining single nestling in the control nest was larger than the largest of the four nestlings in the experimental brood. We directly observed the three control nestlings lose mass and found them impaled in the nest-supporting cactus below the nest, suggesting their deaths were due to starvation and possibly siblicide or suicide (sensu Mock 1984). One of the nestlings found impaled was still alive and was replaced in the nest only to be found impaled in the same place and dead the next day. When this nest pair is excluded from analysis the comparison between largest nestlings in food-supplemented vs. control nests in 1987 becomes significant ($P = .003$). Therefore, most of the food-supplemented nestlings were larger than their controls by 15 d of age in both years.

In 1986, the greater mass of food-supplemented nestlings was also reflected by larger size in all morphological measures (Fig. 3). In 1987, none of the morphological features differed significantly between food-supplemented and control nests (Fig. 3), despite larger masses of nestlings.

*Survivorship of young.*—Number of young present after hatching was equal for both food-supplemented and control nests (42 in each group for both years). Therefore, survivorship differences between food-supplemented and control groups are expressed by differences in the total number of young surviving. Predation was the presumed cause whenever complete broods disappeared, and these nests were excluded from analysis. We assumed that disappearance of some but not all of the nestlings in a brood was due to starvation. This assumption was supported by the observation of starvation described above and an observation at another nest of a parent Cactus Wren carrying a pre-

TABLE 2. Climatic data taken from Sky Harbor Airport monthly summaries. (A) Departure of monthly average temperature (maximum − minimum) from 30-yr monthly average (in °C), and (B) number of days with maximum temperature ≥32°C for breeding season months in 1986 and 1987.

| | Jan | Feb | Mar | Apr | May | Jun | Total |
|---|---|---|---|---|---|---|---|
| A) | | | | | | | |
| 1986 | +5.1 | +2.7 | +4.8 | +3.4 | +2.9 | +3.5 | +22.4 |
| 1987 | +1.3 | +2.0 | +1.6 | +5.5 | +3.1 | +3.6 | +17.1 |
| B) | | | | | | | |
| 1986 | 0 | 4 | 8 | 10 | 25 | 30 | 77 |
| 1987 | 0 | 0 | 0 | 19 | 24 | 30 | 73 |

Table 3. Percentage of clutches laid by Cactus Wrens during each month of two breeding seasons.

| | Percentage of clutches | | | | Laying date variable* | Number of clutches |
|---|---|---|---|---|---|---|
| | Feb | Mar | Apr | May | | |
| 1986 | 0.03 | 52.3 | 35.4 | 10.8 | 32.5 ± 4.8 | 62 |
| 1987 | 0 | 37.8 | 62.2 | 0 | 38.0 ± 3.7 | 37 |

* The mean number of days after 24 February when the first egg was laid in each clutch.

sumably dead nestling out of the nest while other nestlings survived within.

In 1986, the number of nestlings that survived to 15 d of age in food-supplemented nests (40) was marginally greater ($P = .078$, Wilcoxon paired signed-ranks test) than in control nests (34). In 1987, the number of 15-d-old nestlings in food-supplemented nests (37) was not significantly greater ($P = .25$, Wilcoxon paired signed-ranks test) than for control nests (33).

The number of young surviving the first 4–6 wk after fledging in 1986 was greater from food-supplemented (15) than control (7) nests ($P = .047$, Wilcoxon paired signed-ranks test). In 1987, fledgling survivorship was not significantly greater from food-supplemented (19) than control (16) nests ($P = .125$, Wilcoxon paired signed-ranks test).

*Renesting attempts.*—Among the food-supplemented pairs, 12 out of 14 began renesting between 4 and 15 d after their first nest fledged. All but one of these new nests contained nestlings 4 wk after fledging of the previous nest; one nest was depredated by the 4-wk census. Only 7 out of the 14 control pairs began renesting between 7 and 19 d after fledging of their first nest.

Food-supplemented nests showed a higher incidence of renesting at the 4-wk census (12/14) than control nests (7/14) ($P < .05$, $G$ test). The number of days after fledging when renesting began was not different between treatments (Wilcoxon paired signed-ranks test, $P > .05$). All new nests had a clutch size of three, as did most of the first nests of each season. Second nests of the season were not monitored through completion, thus their success at producing young cannot be addressed. There was no relationship between pairs renesting and the amount of supplemental food used, the size or number of young fledging from the first nest, or survival of fledglings.

## DISCUSSION

### *Food limitation*

Results provided here support the contention that Cactus Wrens reproduce at a level that incurs food limitation. Food availability clearly limited reproduction during the nestling and fledgling stages in 1986 as indicated by higher food delivery rates, greater mass and linear dimensions of nestlings, and particularly by the greater survival of fledglings that were supplementally fed. Greater rates of food delivery and increased nestling mass with supplemental feeding in 1987 suggested that food was limiting to some extent in that year as well. However, experimental nestlings were not larger in linear dimensions and did not survive significantly better than control young in 1987, suggesting that food limitation was less severe in 1987.

Comparisons of control nestlings between the 2 yr also suggest that food limitation was less severe in 1987 than 1986. Nestlings had greater masses at 15 d of age and exhibited higher survival rates 4–6 wk after fledging in 1987 than 1986.

The increased frequency of renesting with food supplementation in 1987 indicates that food limited reproduction in that year despite less effects on nestling growth than in the previous year. Supplemental food presumably reduced the energy costs of producing first broods, thus allowing more parents to lay second broods. Such results emphasize the importance of food

Table 4. Composition of nestling diets in control nests.

| | 1986 | | | 1987 | | |
|---|---|---|---|---|---|---|
| | % by number | % by volume | Volume per item ($mm^3$) | % by number | % by volume | Volume per item ($mm^3$) |
| Lepidoptera, larvae (caterpillars) | 40.7 | 33.7 | 190 | 19.2 | 13.9 | 238 |
| Orthoptera (grasshoppers) | 31.0 | 32.7 | 242 | 71.0 | 69.2 | 322 |
| Lepidoptera, adults (moths) | 10.2 | 5.5 | 123 | NP* | NP | NP |
| Coleoptera, larvae (beetle larvae) | 7.6 | 4.7 | 141 | 3.1 | 1.7 | 177 |
| Diptera, adults (flies) | 4.2 | <1 | 49 | 3.6 | <1 | 76 |
| Odonata (dragonflies) | 2.1 | 1.5 | 160 | 2.1 | <1 | 130 |
| Others | <2 | <2 | | <1 | <1 | |
| Total number of items | | 381 | | | 193 | |
| Number of hours sampled | | 60 | | | 31 | |

* NP = not present.

TABLE 5. One-way analyses of variance of mass at fledging in birds that survived vs. those that did not survive for 4 wk after fledging.

| Source | Sum of squares | df | Mean square | *F* | *P* |
|---|---|---|---|---|---|
| | | 1986 | | | |
| Survival | 54.052 | 1 | 54.052 | 4.714 | .033 |
| Error | 917.356 | 80 | 11.467 | | |
| | | 1987 | | | |
| Survival | 0.023 | 1 | 0.023 | 0.004 | .950 |
| Error | 424.578 | 72 | 5.897 | | |

limitation on both present and future reproduction (also see von Bromssen and Jansson 1980, Rodenhouse 1986).

We demonstrated that food limited normal levels of reproduction in Cactus Wrens, suggesting that brood sizes may have evolved to allow parents to take advantage of periods when food is more abundant. This strategy may be advantageous because primary production is highly unpredictable in deserts (Noy-Meir 1973).

The fact that food supplementation only during the nestling period yielded these results indicates that feeding nestlings is an important constraint on reproduction as originally postulated by Lack (1947). However, we cannot compare the importance of the nestling stage to the egg production, incubation, or fledgling feeding stages. Several studies suggest that food levels are also important during egg production and incubation (for review see Martin 1987). To compare the importance of these stages in the nesting cycle food should be supplemented during each stage separately in the same population, as suggested by Hochachka and Boag (1987).

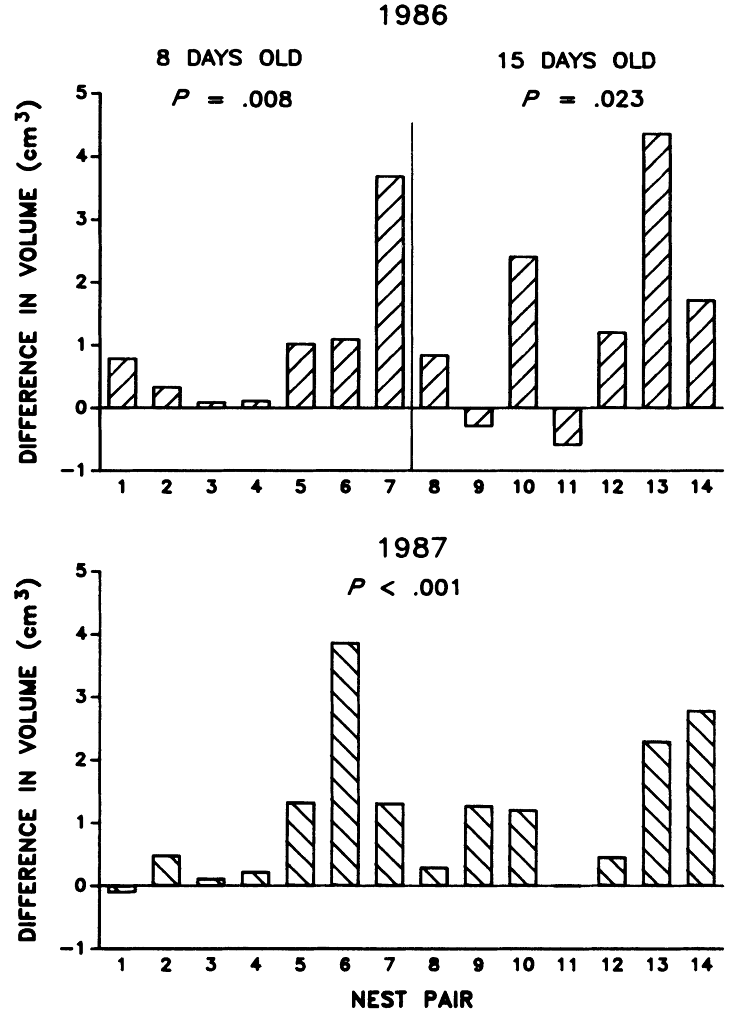

FIG. 1. Differences between treatments (food-supplemented minus control) in volume of food delivered per nestling during a 2-h sampling period. For 1986, the first seven nest pairs were sampled at 5–8 d of age while the last seven were sampled at 11–15 d of age. In 1987, all nest pairs were sampled at 12–15 d of age except for the first two pairs, which were sampled at 8 d of age. Wilcoxon paired signed-ranks tests (one-tailed) were used separately on the two age classes in 1986 while all pairs were tested together for 1987 data.

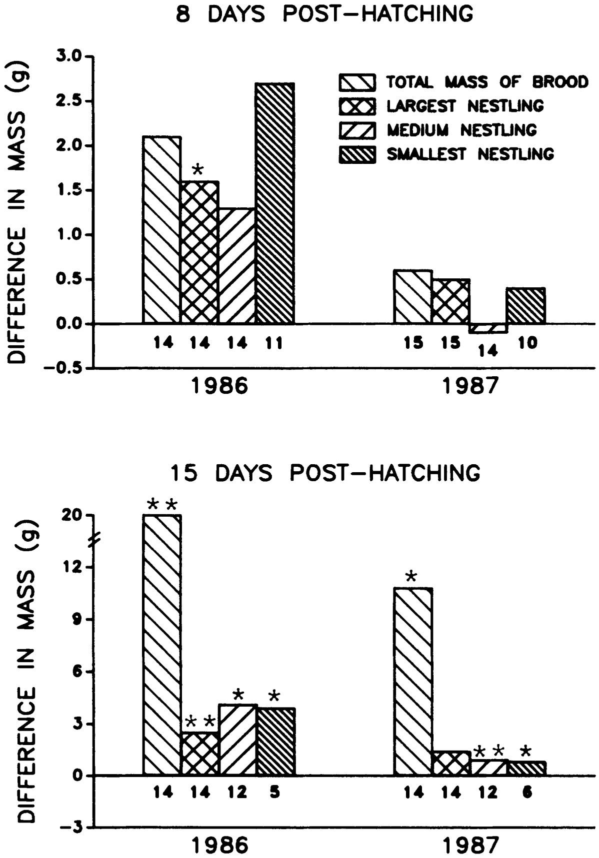

FIG. 2. Differences between treatments (food-supplemented minus control) in measures of nestling mass are presented as averages over all nest pairs. Wilcoxon paired signed-ranks tests (one-tailed) were used to provide the following significance levels: *$P < .05$, **$P < .01$. Sample sizes are provided below each bar.

### *Annual variation*

It is not clear why food limitation was more intense in 1986 than 1987. Differences in food availability between the 2 yr are indicated by differences in food composition of nestlings (Table 4). However, direct sampling of insect prey was not attempted. Insect prey were probably more abundant in 1986 than 1987 because winter precipitation was greater in 1986 (Table 1) and production of desert plants increases with winter precipitation (Norton 1974). Indeed, winter precipitation was positively related to grasshopper abundance in the Chihuahuan Desert (Marr and Raitt 1983).

Surprisingly, food limitation of Cactus Wren reproduction was more intense in 1986, when food abundance was probably greater. This unexpected result may be explained by the differences in bird breeding densities between the 2 yr. Cactus Wren and Curve-billed Thrasher breeding densities were greater in 1986 than 1987. Fifty-two nesting territories of Cactus Wrens were found in 1986, while only 40 were found in 1987. Similarly, 21 Curve-billed Thrasher nests were found in 1986 and only 11 in 1987. We suggest that density-dependent effects such as increased time spent defending territories from other Cactus Wrens or warding off interference from Curve-billed Thrashers more than offset the increased food availability in 1986.

Similarly, Anderson and Anderson (1973) found the highest incidence of successful clutches in Cactus Wrens after a winter of low rainfall and a poor growth of annual plants. Interestingly, nesting density was relatively low that year though data are insufficient to assess a relationship.

Alternatively, the earlier onset of high temperatures in 1986 could have been solely responsible for the greater intensity of food limitation in 1986. Activity of Cactus Wrens significantly declines when temperatures rise above 32° C in the Sonoran Desert (Ricklefs and Hainesworth 1968). Therefore, higher temperatures in 1986 may have limited foraging activity of parents more than in 1987. However, by the time nestling feeding occurred, in April and May, 1986 was not warmer than 1987 (Table 2).

Other studies have suggested that food limitation

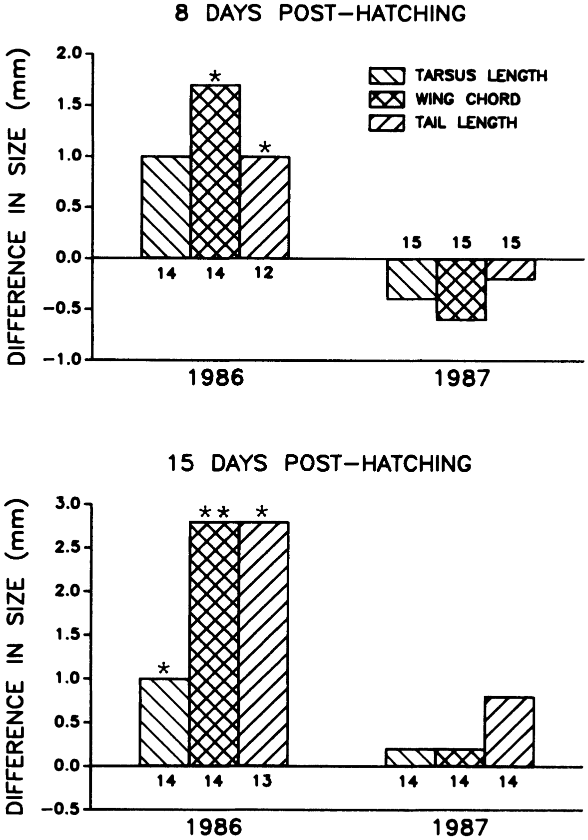

FIG. 3. Differences between treatments (food-supplemented minus control) in mean linear measurements of nestlings are presented as averages over all nest pairs. Wilcoxon paired signed-ranks tests were used to provide the following significance levels: *$P < .05$, **$P < .01$. Sample sizes are provided below each bar.

and competition occur intermittently and only during periods of low food abundance (Wiens 1977). In contrast, our data indicate that food limitation existed in two consecutive years and was greater in magnitude when food abundance was higher. Finally, we suggest that competition intensified food limitation when food availability was relatively high.

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