

## EXPERIMENTAL STUDIES OF NEST-DESTROYING BEHAVIOR BY CACTUS WRENS<sup>1</sup>

Laurie Stuart Simons<sup>2</sup> and Lee H. Simons<sup>3</sup>

Department of Zoology, Arizona State University, Tempe, AZ 85287

**Abstract.** We studied nest-destroying behavior in Cactus Wrens (*Campylorhynchus brunneicapillus*) using experimental nests containing Japanese Quail (*Coturnix japonica*) eggs. Because wrens did not consume the egg contents, the behavior is not predation. Wrens attacked nests only within their own territories but often in vegetation not used as nesting substrate. Hence, the behavior probably does not represent attempts at cuckoldry or mate displacement, or competition for nest sites. Nest destruction may represent intraspecific or interspecific competition for (1) food or (2) predator-free nesting space. Evidence supporting these nonexclusive hypotheses are that food limits reproductive success in this population of wrens, and nest predation was density dependent in this population (natural nests surrounded by experimental nests showed higher predation rates than controls). Major predators included snakes, especially whipsnakes (*Masticophis* spp.), which are able to access Cactus Wren nests despite cholla (*Opuntia* spp.) spines.

**Key words:** Cactus Wren; *Campylorhynchus brunneicapillus*; nest destruction; nest competition; nest predation; egg destruction; snakes.

### INTRODUCTION

Several species of wrens (Family Troglodytidae) destroy conspecific or heterospecific eggs or nestlings; this behavior is known in Marsh Wrens (*Cistothorus palustris*), House Wrens (*Troglodytes aedon*), Sedge Wrens (*C. platensis*), Bewick's Wrens (*Thryomanes bewickii*), Rufous-and-white Wrens (*Thryothorus rufalbus*), and Cactus Wrens (*Campylorhynchus brunneicapillus*) (Allen 1914; Kendeigh 1941; Anderson and Anderson 1973; Picman 1977a, 1977b, 1984; Picman and Picman 1980; Belles-Isles and Picman 1986; Freed 1987). Because nest destroyers invest time and risk reprisal from nest owners, they probably derive compensatory benefit(s). Yet the adaptive significance of nest destruction is poorly understood.

Wrens apparently derive no direct nutrition from nest destruction since they do not seem to consume egg contents or nestlings (Sherman 1925; Anderson and Anderson 1973; Picman 1977a, 1977b; Picman and Picman 1980; Belles-Isles and Picman 1986; pers. observ.). Nest destruction by nonresident wrens might provide op-

portunities for cuckoldry or pair or mate displacement during renesting. Nest destruction may also represent intra- or interspecific competition for nest sites (Kendeigh 1941, Belles-Isles and Picman 1986), or food (Picman 1977a, Belles-Isles and Picman 1986, Freed 1987), or predator-free nesting space (Tinbergen et al. 1967, McGee 1985). We explored these alternatives by observing free-living Cactus Wrens as they responded to experimental nests, and by testing for density-dependent nest predation in a population of Cactus Wrens.

### METHODS AND RESULTS

We worked in Sonoran Desert scrub habitat within Usery Mountain Park, Maricopa County, Arizona. Cactus Wrens in the Sonoran Desert prefer to nest in cholla cacti (*Opuntia* spp.), but will also nest in saguaro cacti (*Carnegie giganteus*), palo verde (*Cercidium* spp.), or other spiny plants (Anderson and Anderson 1973, McGee 1985). Cactus Wrens typically build two to five "secondary" nests within about 15 m of their active nest (Anderson and Anderson 1973, pers. observ.). Parents roost in secondary nests, but often build more nests than required for this purpose. Secondary nests presumably serve some additional purpose, such as roosting sites for offspring or to decoy predators (Anderson and Anderson 1973).

Some of our experimental nests were natural Cactus Wren nests imported from outside the

<sup>1</sup> Received 20 November 1989. Final acceptance 28 June 1990.

<sup>2</sup> Present address: Endangered Species Office, U.S. Fish and Wildlife Service, 2800 Cottage Way, Sacramento, CA 95825.

<sup>3</sup> Present address: Center for Population Biology, Storer Hall, University of California, Davis, CA 95616.

study area, but most (80%) were artificial nests constructed from straw, string, and wallpaper paste. These artificial nests varied from nearly enclosed (like Cactus Wren nests) to nearly completely open (like Curve-Billed Thrasher, *Toxostoma curvirostre*, nests). Use of natural vs. artificial nests was randomized across treatments and time, and both types were attacked equally by Cactus Wrens.

The modal number of eggs in natural Cactus Wren clutches at our study site was three ( $n = 99$ ; range = 2–4). Consequently, we always used three Japanese Quail eggs (*Coturnix japonica*) to simulate breeding activity in experimental nests. Quail eggs are similar in shape and color to Cactus Wren eggs and only slightly larger in size (ca. 25 × 30 mm vs. 16 × 25 mm). All fieldwork was conducted during the nesting seasons (April–June) in 1986 and 1987. We used *G*-tests of independence to compare frequencies and a *t*-test to compare the number of human visits to natural nests with and without experimental nests (Sokal and Rohlf 1981). For all tests a 5% alpha level was considered significant.

#### BEHAVIORAL OBSERVATIONS OF NEST ATTACKS

We expected that if nest destroyers were territorial intruders, then experimental nests placed far from active nests would be attacked preferentially because such areas are probably defended less vigorously by resident Cactus Wrens. Alternatively, if nest destroyers were territorial owners, then experimental nests placed near active nests would be more quickly attacked because such areas are probably defended more vigorously. Thus, to determine the identity of nest destroyers, we placed single experimental nests in cholla at three distances from the same active natural nest: 5 to 10 m, 20 to 25 m, and 45 to 50 m. Nests were placed between 06:00 and 09:00 and simultaneously watched for 1 hr from a concealed position using field glasses.

We replicated this experiment nine times before and 11 times after eggs were laid in natural nests. After the first eight replicates (all pre-egg stage), we established a fourth nest-placement position very close to active nests (1–2 m) that was continued in all subsequent replications. This fourth position was established to discern, if possible, any effect of proximity to the active nest on nest destruction, which had not been evident from comparison of early results at the inter-

mediate distances. Due to a lack of cholla in the 5–10 m range, one postlaying replicate also lacked an experimental nest at that distance. Thus, a total of 71 “nest by distance” observations were performed. We focused each replicate around a different natural nest to avoid possible effects of experience, and removed experimental nests after each observation period.

We often observed Cactus Wrens investigating or pecking eggs within 2 or 3 min after placement. In all except two replicates (both pre-egg stage), at least one territorial owner investigated at least one experimental nest by perching on or near, and orienting toward, the nest. In only 10 of 20 observation periods, however, were experimental nests actually attacked. Of 14 Cactus Wrens observed actually attacking nests, all were territorial owners based on color bands, nest attendance, or territorial singing. Frequency of nest-destroying behavior was independent of distance from the natural nest (Table 1,  $P > 0.10$ ), whether or not territorial owners had laid their own eggs (Table 2,  $P > 0.10$ ), or sex of the attacker ( $P > 0.9$ ). Eight of 18 males (44%) that investigated experimental nests also attacked eggs, while six of 15 investigating females (40%) also attacked eggs. Nesting material was often removed from experimental nests, but only by wrens that also pecked eggs.

#### EFFECT OF NEST SUBSTRATE AND SECONDARY NESTS

We compared loss rates of eggs in experimental nests set in four configurations to test if nest substrate or the presence of empty secondary nests influence the probability of nest attack. Single nests, each with three eggs, were placed in cholla (*Opuntia fulgida*), palo verde (*Cercidium microphyllum* or *C. floridum*), or jojoba (*Simmondsia chinensis*). Cholla and palo verde are spiny whereas jojoba lacks spines. In the fourth configuration, five nests were set in cholla within a 10-m diameter, but only one nest contained eggs. The nest with eggs was determined randomly to simulate an active nest in the vicinity of four secondary nests. This configuration reflects the situation often observed in nature (Anderson and Anderson 1973; pers. observ.).

These four experimental configurations were alternated at 50-m intervals along a transect through Cactus Wren nesting habitat until each arrangement was replicated 11 times. No two experimental nests of the same treatment type

TABLE 1. The number of experimental nests that Cactus Wrens either attacked or investigated but did not attack at four distances from active Cactus Wren nests during the first hour after placement of experimental nests. There is no significant effect of distance from the active nest (*G*-test,  $P > 0.05$ ).

Distance from active Cactus Wren nest (m)	Number of nests placed	Number attacked	Number investigated but not attacked
1-2	12	2	10
5-10	19	7	10
20-25	20	7	11
45-50	20	2	16
Total	71	18	47

were placed in the same wren's territory because territory size was 1 to 2 ha (pers. observ.). Nests were checked 7, 15, and 24 days after establishment for evidence of nest attack. Nests were considered attacked if any eggs were broken or removed. Although some egg losses may have been due to predators or other causes, most were due to Cactus Wrens because eggs were often found with holes in them the size of those known to be made by Cactus Wrens, and because Cactus Wrens were sometimes observed investigating nests.

Nest attacks were prevalent in all configurations, exceeding 30% after 1 week and 70% after 2 weeks (Fig. 1). Nearly all eggs had been attacked by the third survey. The number of experimental nests attacked did not differ significantly among nest substrates ( $P > 0.10$ ). Experimental nests with and without secondary nests were also attacked at similar frequencies ( $P > 0.10$ ).

EFFECTS OF NESTING DENSITY ON NEST PREDATION

Because we removed experimental nests immediately after observations in our first experiment, the effect of increased density of nests on survival of natural nests was not observed. To test if nest predation was density-dependent in this Cactus Wren population, we conducted another experiment wherein we placed and left experimental nests containing eggs in cholla at three distances from the same active Cactus Wren nest: 5 to 10 m, 20 to 25 m, and 45 to 50 m. We replicated this experiment in nine different Cactus Wren territories containing natural nests in the incubation stage. To serve as controls, we observed concurrently nine other natural Cactus Wren nests

TABLE 2. The number of male and female Cactus Wrens that attacked experimental nests vs. those that investigated but did not attack experimental nests before and after females laid eggs. Attack frequency was independent of whether Cactus Wrens had laid their eggs (*G*-test,  $P > 0.10$ ).

Female stage	Males		Females	
	Attack	No attack	Attack	No attack
Pre-egg laying	3	4	2	3
Post-egg laying	5	6	4	6
Total	8	10	6	9

in the same stages of development but without experimental nests around them. We examined all experimental and natural nests at 2, 4, 8, and 12 days after starting the experiment for evidence of nest destruction or predation. Predation was presumed to occur on natural nests when the total clutch or brood was lost between nest checks. Because human visitation could influence nest predation, we also compared the number of human visits to natural nests that were or were not surrounded by experimental nests.

Frequency of predation on natural Cactus Wren nests increased greatly with the addition of experimental nests (Table 3,  $P < 0.005$ ). Nest destruction of experimental nests was again independent of distance from the natural nest ( $P > 0.10$ ). The number of human visits to natural nests with and without experimental nests did not differ significantly ( $\bar{x} \pm SE = 15.1 \pm 3.02$  and  $13.4 \pm 4.42$ , respectively,  $P = 0.619$ ,  $n = 9$  in each group). Thus, human visitation was probably not responsible for the different levels of predation.

DISCUSSION

NEST DESTRUCTION

All nest attacks that we observed were performed by Cactus Wrens in their own territories. Other wrens also destroy nests within their territories (Belles-Isles and Picman 1986, Picman and Belles-Isles 1987). Since territorial owners rather than unpaired intruders are attacking nests, the behavior apparently does not serve to provide opportunities for cuckoldry or pair or mate displacement. Rather, nest destruction is likely a form of territorial behavior. Resources defended by nest attackers might include food, nest sites, or predator-free nesting space.

Cactus Wrens attack many types of nests in-

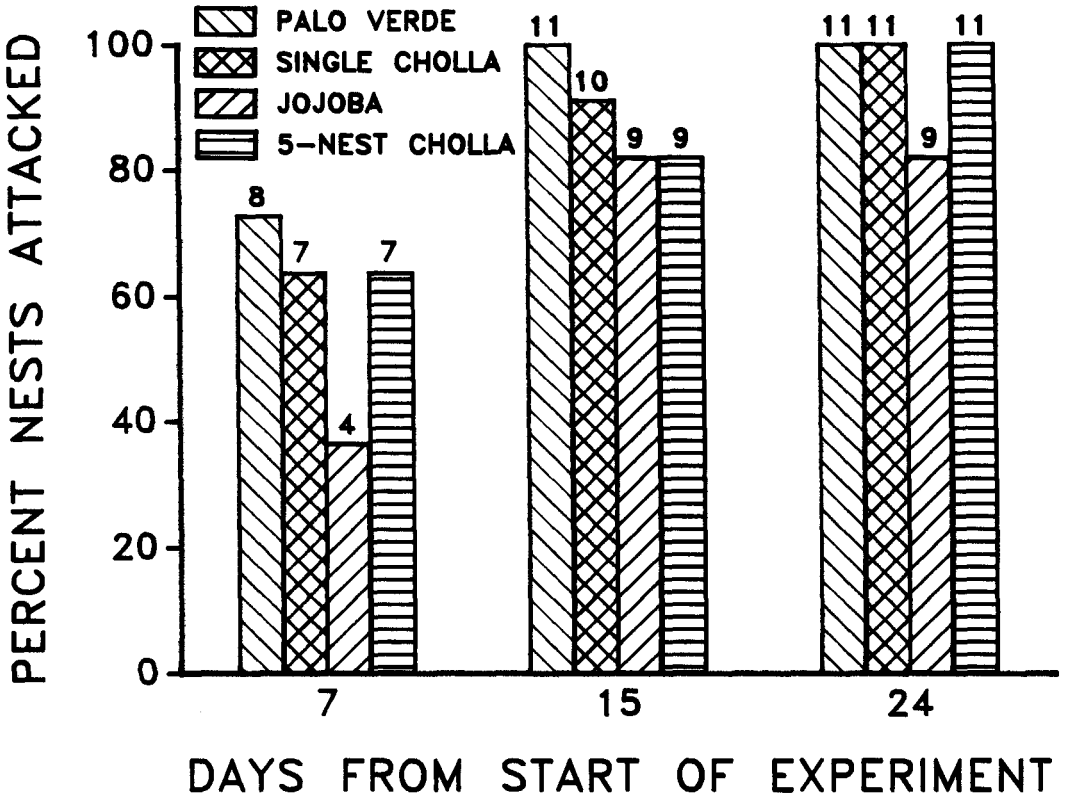


FIGURE 1. Percentage of experimental nests attacked in four configurations at 7, 15, and 24 days after start of the experiment. Configurations included single experimental nests with three eggs in: (1) a palo verde tree, (2) a cholla cactus, (3) a jojoba bush, or (4) a cholla cactus surrounded by four empty secondary nests also in cholla. Numbers above bars represent number of nests attacked (eggs removed or damaged) in each group. Attack frequency was independent of nesting substrate or the presence of empty secondary nests ( $G$ -tests,  $P > 0.10$ ).

cluding House Sparrow (*Passer domesticus*) and House Finch (*Carpodacus mexicanus*) nests that are open and cup-shaped (Anderson and Anderson 1973), and Verdin (*Auriparus flaviceps*) nests that are enclosed but much smaller than Cactus Wren nests (Taylor 1971, McGee 1985). We ob-

TABLE 3. Summary of predation frequency of natural Cactus Wren nests with and without experimental nests placed in the territory. Predation frequency was significantly greater in nests with experimental nests added than without ( $G$ -test,  $P < 0.005$ ).

	With experimental nests	Without experimental nests
Depredated	5	0
Not depredated	4	9
Total	9	9

served Curve-Billed Thrasher eggs with holes equal in size to those pecked in experimental quail eggs by Cactus Wrens. Thus, Cactus Wrens seem to attack both conspecific and heterospecific nests.

Nest attacks may serve to reduce competition for food since food is known to limit reproduction of Cactus Wrens in this population (Simons and Martin 1990). Like Cactus Wrens, Curve-Billed Thrashers and House Finches forage for ground insects, and Verdins glean insects from vegetation. We also observed frequent behavioral interference between Cactus Wrens and Curve-Billed Thrashers at artificial feeders and natural (cactus fruit) food sources.

Nest destruction by Cactus Wrens apparently does not reflect intra- or interspecific competition for nest sites, as suggested for House Wrens

(Belles-Isles and Picman 1986). Cactus Wrens destroyed experimental nests in jojoba (Fig. 1), yet jojoba is not used by Cactus Wrens as a nesting substrate. Experimental nests in jojoba were attacked at frequencies equal to experimental nests in preferred (cholla) and somewhat less preferred (palo verde) nesting substrates. Furthermore, potential nest sites generally seem plentiful in Cactus Wren territories (McGee 1985). Thus, nest destruction probably does not reflect competition for nest sites per se, but may reflect competition for predator-free nesting space.

If predators are attracted to areas of high nesting density, Cactus Wrens may destroy a variety of nests to decrease nesting density and ultimately predation pressure in their own territory (Fretwell 1972, McGee 1985, Martin 1988b). In this sense, Cactus Wrens may compete for predator-free nesting space with conspecifics or heterospecifics that encroach on their territories (Martin 1988a, 1988b). In keeping with this hypothesis, nest destruction always occurred within the attacker's territory in this study. This explanation is also supported by our result that nest predation is density dependent in this population (Table 3).

Although eggs within experimental nests were generally punctured quickly by Cactus Wrens, many of these eggs remained in the nest or on the ground below the nest where they could attract predators. The fact that predators responded to experimental nests despite these nests having been quickly attacked, suggests that nest-destroying behavior may not serve so much to rid an area of nests already constructed (though this may also be important), as to prevent the establishment of additional nests to begin with. The "threat" of nest destruction may be sufficient to dissuade other birds from nesting near Cactus Wren nests (but see next section).

The similarity in loss rate of experimental nests with and without secondary nests suggests that secondary nests did not deter nest destroyers. However, because "active" nests in this experiment were not defended by a resident pair of birds, secondary nests may not have yielded the benefit they might under natural situations. If secondary nests slow down potential nest destroyers long enough for nest owners to detect and deter the threat, then lack of defending birds in our experiment largely obviates the usefulness of secondary nests. On the other hand, because Cactus Wrens are visually oriented, the activity

of nest caretakers may attract attention, possibly increasing nest destruction rates. These factors are to some degree offsetting, and it would be interesting to repeat this experiment using real active nests that are defended.

#### INHIBITION OF NEST DESTRUCTION

In our experiments, the frequency of nest destruction by Cactus Wrens was relatively low in experimental nests very close to natural nests. Apparently, nest-destroying behavior is inhibited very close to destroyers' own nests. Analogous inhibitions of nest-destroying behavior are reported for House Wrens, which do not attack experimental nests after pairing (in males) or laying (in females) (Belles-Isles and Picman 1986). House Wrens may suspend nest attacks to avoid destroying their own eggs accidentally, or to lessen interference from other birds during nesting (Belles-Isles and Picman 1986). Likewise in Marsh Wrens, destruction of conspecific nests is inhibited during nesting (in females) or when a female is present (in males) presumably to avoid killing offspring (Picman and Belles-Isles 1987). In contrast, both sexes of Cactus Wrens attacked experimental nests equally before and after laying their own eggs (Table 2). However, Cactus Wrens may avoid killing offspring or risking reprisal from nest owners by curtailing nest destruction in the immediate vicinity of their own nest. Cactus Wrens occasionally raise and fledge young from nests that are very close or even physically touching active nests of Curve-billed Thrashers or Inca Doves, *Columbina inca* (Anderson and Anderson 1973; pers. observ.).

#### PREDATION

Many kinds of predators in the Sonoran Desert undoubtedly take young birds or eggs at least occasionally, including hawks, owls, roadrunners, mammalian carnivores, snakes, and Gila monsters. Snakes are particularly common in this habitat and are probably one of the most frequent predators of birds (Anderson and Anderson 1973). Near our study site we watched a gopher snake (*Pituophis melanoleucus*) rapidly swallow an entire clutch of 14 Gambel's Quail (*Callipepla gambelii*) eggs, and a Sonoran whipsnake (*Masticophis bilineatus*) capture and eat a fledgling Ash-throated Flycatcher (*Myiarchus cinerascens*). A colleague observed whipsnakes (*M. bilineatus* and *M. flagellum*) preying on Mourning Dove (*Zenaida macroura*) and Verdin nestlings

(C. McElrath, pers. comm.), and there are similar reports in the literature (e.g., Finch 1981, Marr 1985).

On our study site, whipsnakes were frequently observed in cholla, and sometimes within bird nests, including Cactus Wren nests. Yet we never found snakes entrapped in cholla like we occasionally found other species, including rabbits, rodents, bats, humans, and birds, including Cactus Wrens. Whipsnakes are adept at removing cholla joints from their body (not a simple task) through a peculiar rapid rolling behavior (pers. observ.). Cactus Wrens invariably defended their nest sites against model (taxidermy) whipsnakes, by vocalizing, flying, and running within a few meters of the model (Simons, pers. observ.). Finally, nests that had lost entire clutches of eggs or nestlings (presumably due to predation rather than starvation, brood reduction, or siblicide) were often otherwise intact, indicating that eggs or nestlings were removed via the entrance. It is unlikely that predators other than snakes could remove eggs or nestlings without physically destroying the nest (see also Anderson and Anderson 1973).

Competition for predator-free nesting space or for food remain viable and not necessarily exclusive hypotheses for why Cactus Wrens destroy nests. Additional work, including more observations and experimental quantification of nest predation under a variety of nest dispersions and habitat conditions (e.g., Picman 1988), is needed to test these hypotheses further.

#### ACKNOWLEDGMENTS

We thank J. Roper, K. Donohue, and personnel of the Maricopa County Parks and Recreation Department for field assistance, S. Clarkson and T. Roudybush for providing quail eggs (courtesy the Department of Avian Sciences, University of California, Davis), and T. E. Martin, M. Moore, J. Picman, D. Rasmussen, S. M. Russell, R. Rutowski, G. Walsberg, and an anonymous reviewer for manuscript review. Support was provided by the Department of Zoology and Graduate Student Association at Arizona State University, the Achievement Rewards for College Students (ARCS) Foundation, the Frank M. Chapman Memorial Fund, and Sigma Xi—The Scientific Research Society.

#### LITERATURE CITED

- ALLEN, A. A. 1914. The Red-Winged Blackbird: a study in the ecology of a cattail marsh. Proc. Linn. Soc. N.Y. 52/53:75–83.

- ANDERSON, A. H., AND A. ANDERSON. 1973. The Cactus Wren. Univ. of Arizona Press, Tucson.
- BELLES-ISLES, J., AND J. PICMAN. 1986. House Wren nest-destroying behavior. Condor 88:190–193.
- FINCH, D. 1981. Nest predation of Abert's Towhees by coachwhips and roadrunners. Condor 83:389.
- FREED, L. A. 1987. Rufous-and-white Wrens kill House Wren nestlings during a food shortage. Condor 89:195–197.
- FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton Univ. Press, Princeton, NJ.
- KENDEIGH, S. C. 1941. Territorial and mating behavior of the House Wren. Ill. Biol. Monogr. 18: 1–20.
- MARR, N. V. 1985. Gopher snake preys on Northern Oriole nestlings. Murrelet 66:95–97.
- MARTIN, T. E. 1988a. Processes organizing open-nesting bird assemblages: competition or nest predation? Evol. Ecol. 2:11–24.
- MARTIN, T. E. 1988b. On the advantage of being different: nest predation and the coexistence of bird species. Proc. Natl. Acad. Sci. 85:2196–2199.
- MCGEE, M. 1985. Interspecific nest interference: the influence of Cactus Wrens (*Campylorhynchus brunneicapillus*) on Verdins (*Auriparus flaviceps*) nest site selection. M.Sc. thesis, Univ. of Arizona, Tucson.
- PICMAN, J. 1977a. Destruction of eggs by the Long-billed Marsh Wren (*Telmatodytes palustris palustris*). Can. J. Zool. 55:1914–1920.
- PICMAN, J. 1977b. Intraspecific nest destruction in the Long-billed Marsh Wren, *Telmatodytes palustris palustris*. Can. J. Zool. 55:1997–2003.
- PICMAN, J. 1984. Experimental study on the role of intra- and inter-specific competition in the evolution of nest-destroying behavior in Marsh Wrens. Can. J. Zool. 62:2353–2356.
- PICMAN, J. 1988. Experimental study of predation on eggs of ground-nesting birds: effects of habitat and nest distribution. Condor 90:124–131.
- PICMAN, J., AND J. BELLES-ISLES. 1987. Intraspecific egg destruction in marsh wrens: a study of mechanisms preventing filial ovicide. Anim. Behav. 35: 236–246.
- PICMAN, J., AND A. K. PICMAN. 1980. Destruction of nests by the Short-billed Marsh Wren. Condor 82: 176–179.
- SHERMAN, A. R. 1925. Down with the House Wren boxes. Wilson Bull. 37:5–13.
- SIMONS, L. S., AND T. E. MARTIN. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. Ecology 71:869–876.
- SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry: the principles and practice of statistics in biological research. 2nd ed. W. H. Freeman and Co., San Francisco.
- TAYLOR, W. K. 1971. Breeding biology study of the Verdins, *Auriparus flaviceps* (Sundevall) in Arizona. Am. Midl. Nat. 85:289–328.
- TINBERGEN, N., N. IMPEKOVEN, AND D. FRANCK. 1967. An experiment on spacing-out as a defense against predation. Behaviour 28:307–321.