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**INTERSPECIFIC NEST INTERFERENCE: THE INFLUENCE OF CACTUS  
WRENS (CAMPYLORHYNCHUS BRUNNEICAPILLUS) ON VERDIN  
(AURIPARUS FLAVICEPS) NEST SITE SELECTION**

*The University of Arizona*

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THE INFLUENCE OF CACTUS WRENS (CAMPYLORHYNCHUS BRUNNEICAPILLUS)  
ON VERDIN (AURIPARUS FLAVICEPS) NEST SITE SELECTION

by  
Marie McGee

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A Thesis Submitted to the Faculty of the  
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY  
In Partial Fulfillment of the Requirements  
For the Degree of  
MASTER OF SCIENCE  
In the Graduate College  
THE UNIVERSITY OF ARIZONA

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## ABSTRACT

Desert plants vary greatly in their structural suitability as avian nest sites. This study provides evidence that interspecific nest interference can deter a species from using a preferred nest plant. Verdins and Cactus Wrens both build enclosed, year-round roost nests. Verdins typically nest in spinescent trees and shrubs; Cactus Wrens favor cholla cacti. Cactus Wrens will usurp or destroy Verdin nests. Examination of Verdin nest site selection in Baja California, Mexico and southeastern Arizona revealed: 1) Verdin use of chollas is negatively correlated with Cactus Wren abundance; 2) Verdins often choose chollas preferentially as nest plants; and 3) nesting habitats of the two species diverge as Cactus Wren abundances increase. Often interspecific nest interference in birds is not associated with resource competition. Nest usurping is a parasitic, not competitive, interaction. Nest destruction may be a response to density-dependent nest predation and function to hinder search image formation by mutual predators.

## CHAPTER 1

### INTRODUCTION

#### Nest Site Availability In Desert Scrub Bird Communities

Studies of nest site competition between avian species have generally been restricted to a few groups with obviously specialized nest sites: cavity nesters (e.g. Walkinshaw 1941, 1953; Lack 1954), cliff or shore nesting marine birds (e.g. Stonehouse 1962, Burger and Shisler 1978, Duffy 1983) and large raptors (e.g. Newton 1979). (Also see Snyder 1978.) Among small land birds other than cavity nesters, nest site competition is usually considered unimportant (Ricklefs 1969: 7; Cody 1974: 207-208). This thinking may be based on the implicit assumption that nest site selection by birds is random with respect to plant species (Tomoff 1974, MacArthur and MacArthur 1961) and that suitable nest sites are therefore virtually unlimited (Cody 1974). This may be a reasonable assumption for deciduous forest habitats where the plants representing potential nest sites are relatively uniform in physiognomy (Tomoff 1974). However, careful study reveals that even in deciduous forests some tree species are used often as nest sites by many species while others are structurally unsuitable for nest attachment (Nickell 1958).

In contrast to deciduous forests, desert scrub vegetation includes plants which are conspicuously diverse in structure. Creosotebush (Larrea tridentata) is a widespread shrub which exists as a dominant or subdominant species throughout much of the southwestern deserts. It has long been apparent that structurally uniform habitats dominated by creosotebush support depauperate breeding bird communities while desert scrub habitats of more structural complexity support a greater diversity and density of birds (Anderson and Anderson 1946, Hensley 1954, Dixon 1959, Raitt and Maze 1968, Austin 1970, Tomoff 1974). All of these authors recognized, to some degree, that the availability of suitable nest sites is a critical factor in this relationship. Creosotebush itself is unsuitable as a nest plant (e.g. Anderson and Anderson 1946). With the exception of occasional Black-throated Sparrow (Amphispiza bilineata) nests in the base of the plant (Raitt and Maze 1968, Tomoff 1974), nests built in creosotebush are extremely rare. (Also see Anderson and Anderson 1946; Johnson, Bryant and Miller 1948; and Brown, McGee and Schwalbe MS.) Therefore, few or no birds are found breeding in extensive, pure stands of creosotebush.

Dixon (1959) discussed the positive correlation between the structural diversity in vegetation and the diversity and density of bird species as revealed by his study of the Chihuahuan Desert of western Texas and Hensley's (1954) study of

the Sonoran Desert of southwestern Arizona. Tall yuccas and areas of denser, taller shrubs in Dixon's study area were important to various species of birds as nest sites and/or song perches, foraging sites, or shade.

Raitt and Maze (1968) examined an even less structurally diverse Chihuahuan Desert habitat, a creosotebush dominated community in southern New Mexico. They stressed that it was only the lack of trees or arborescent shrubs which prevented the occurrence of many bird species in their area. Black-throated Sparrows, the most abundant species, were the only birds which utilized creosotebush as nest plants and, therefore, with the exception of ground nesters, the only species which nested away from the taller and more diverse arroyo vegetation. Verdins (Auriparus flaviceps), second in density, were apparently limited only by their need for suitable nest plants, since a pair of Verdins required as few as one spinescent shrub over 4 ft in height to maintain a territory (Raitt and Maze 1968).

Austin (1970) found that for a mesquite bosque and surrounding habitats in the Mohave Desert of southern Nevada, MacArthur and MacArthur's (1961) foliage height diversity index (FHD) was a good predictor of breeding bird diversity. He commented, however, that the usefulness of FHD in desert habitats is limited by the dominance of creosotebush, which contributes

significantly to the foliage volume but is of little use to birds.

Tomoff (1974, also 1971) studied an area of greater physiognomic diversity, the Sonoran Desert of southeastern Arizona. In contrast to Austin's results, Tomoff found that FHD did not consistently predict the bird species diversities of different habitats because it ignored the importance of specific structural elements in the vegetation that are critical as nest sites. In Austin's (1970) study area, mesquites (Prosopis) and creosotebush dominated and at least 95% of nests were placed in mesquites and other spinescent trees. Tomoff's (1974) study area also included arborescent cholla cacti (Opuntia spp., subgenus Cylindropuntia) and saguaros (Carnegiea gigantea) which, although relatively rare, were extremely important as nest sites.

Tomoff's (1974) "physiognomic coverage diversity index" (PCD) is a quantitative measure of the structural complexity of the vegetation. Unlike FHD, PCD was a good predictor of the bird species diversity on Tomoff's study sites. The density of breeding birds on the sites increased in proportion to the density of the types of nest plants they used. Tomoff (1974) suggested that in eastern deciduous forests, unlike the Sonoran Desert scrub, PCD and FHD may be closely correlated, so that a measure of FHD is also a measure of PCD. This may also be true for the habitats studied by Austin (1970) where, as in deciduous

forests, potential nest sites are provided by a group of trees and shrubs which are all of the same basic structural type.

In summary, Tomoff's (1974) results supported the suggestions of many previous authors regarding the important role of nest plant availability in structuring desert scrub bird communities. Desert plants can be categorized into a number of distinctive structural types and birds are highly specific in selecting nest plants from among these. Thus a specific type of nest plant is a critical resource which may limit the distribution of breeding birds. In contrast to the structurally homogeneous plants available to birds in deciduous forests, nest plants of desert scrub habitats are more likely, therefore, to become the focus of competitive interactions.

#### Nesting Requirements and Nest Site Selection in Two Desert Birds

Verdins and Cactus Wrens (Campylorhynchus brunneicapillus) are two resident desert scrub birds which have widely overlapping ranges and habitats and very similar nesting requirements. Both species build enclosed, globular to retort shaped nests and each individual requires a roosting nest in all seasons. Verdins typically build in a wide variety of spinescent desert trees and shrubs while Cactus Wrens rely heavily on cholla cacti as nest sites.

Cactus Wrens interfere with Verdin nesting by usurping and destroying nests and by stealing nest materials (Anderson and Anderson 1934, 1973; Moore 1965; Taylor 1971; personal observations). Taylor (1971) documents 12 instances of Verdin nests, previously in use by Verdins, being either usurped as roosts or completely destroyed by Cactus Wrens. Nests appropriated by the wrens have an enlarged entrance and are often modified with additional nesting materials.

When a Cactus Wren approaches a Verdin nest, Verdins become very agitated, scold, and attempt to drive the wren from the area (Taylor 1971, personal observations). Taylor described these encounters as the most frequent and vigorous interactions in which Verdins were involved. Cactus Wrens, however, are much larger birds than Verdins (38.9 g versus 6.8 g, Dunning 1984) and appear to be deterred very little by the aggressive behavior of Verdins (personal observations).

Arborescent cholla cacti represent an important source of nest sites in Sonoran desert scrub habitats. Many bird species utilize cholla and it is the conspicuously favored nest site of a number of species, including Cactus Wrens. Tomoff (1974), for example, found that in one study area with 11 species of breeding birds, 86 % of all the nests (N=37) were in chollas, although chollas made up only 2.5 % of the total plant density.

I found that in the deserts of central Baja California, Mexico, Verdins show a strong tendency to nest in chollas, not in trees and shrubs as is typical in Arizona and elsewhere. Cactus Wrens are concentrated in the mesic canyons and at higher altitudes and are relatively uncommon in the central desert area. (See also Bancroft 1930.) The similarities in the nests and nesting requirements of these two species, the documented interference of Verdin nesting activities by Cactus Wrens, and the strong preference of Cactus Wrens for cholla nest sites suggested that the utilization of cholla by Verdins in Baja California reflects ecological release due to a mitigation of aggressive interference by Cactus Wrens.

I studied the influence of Cactus Wren abundance and of nest plant availability on the nest site selection of Verdins in Baja California and in southeastern Arizona to address the following questions: 1) Is Verdin usage of cholla nest sites negatively correlated with local abundance of Cactus Wrens? 2) Are cholla cacti preferred as nest plants by Verdins? and 3) Does habitat use of the two species diverge as Cactus Wren abundances increase?

## CHAPTER 2

### METHODS

#### Study Sites

I examined Verdin nest site selection, Cactus Wren abundance, and nest plant availability at 8 locations throughout the peninsula of Baja California, Mexico, and 3 locations in the vicinity of Tucson, Arizona (Fig. 1). In the arid Southwest, considerable differences often exist between the vegetation and fauna associated with the relatively mesic, intermittent desert watercourses (washes or arroyos) and those of the xeric surrounding habitats. Both habitat types were examined at some locations, giving a total of 12 Baja California and 5 Arizona study sites. The locations of the study areas and the habitat type(s) examined at each are listed in Table 1. Data were collected between November 1981 and August 1982.

Figure 1 is a map of the region encompassed by this study with the study areas located. For comprehensive discussions of the vegetation and climate of these areas see Shreve (1951, 1937), Brown (1982a) and Anderson and Anderson (1973: 13-17). With the exception of the southernmost site, all the study sites are within subdivisions of the Sonoran Desert as defined by Shreve (1951). The southernmost site (SHIP) is located in the Cape district of Baja California. Although the

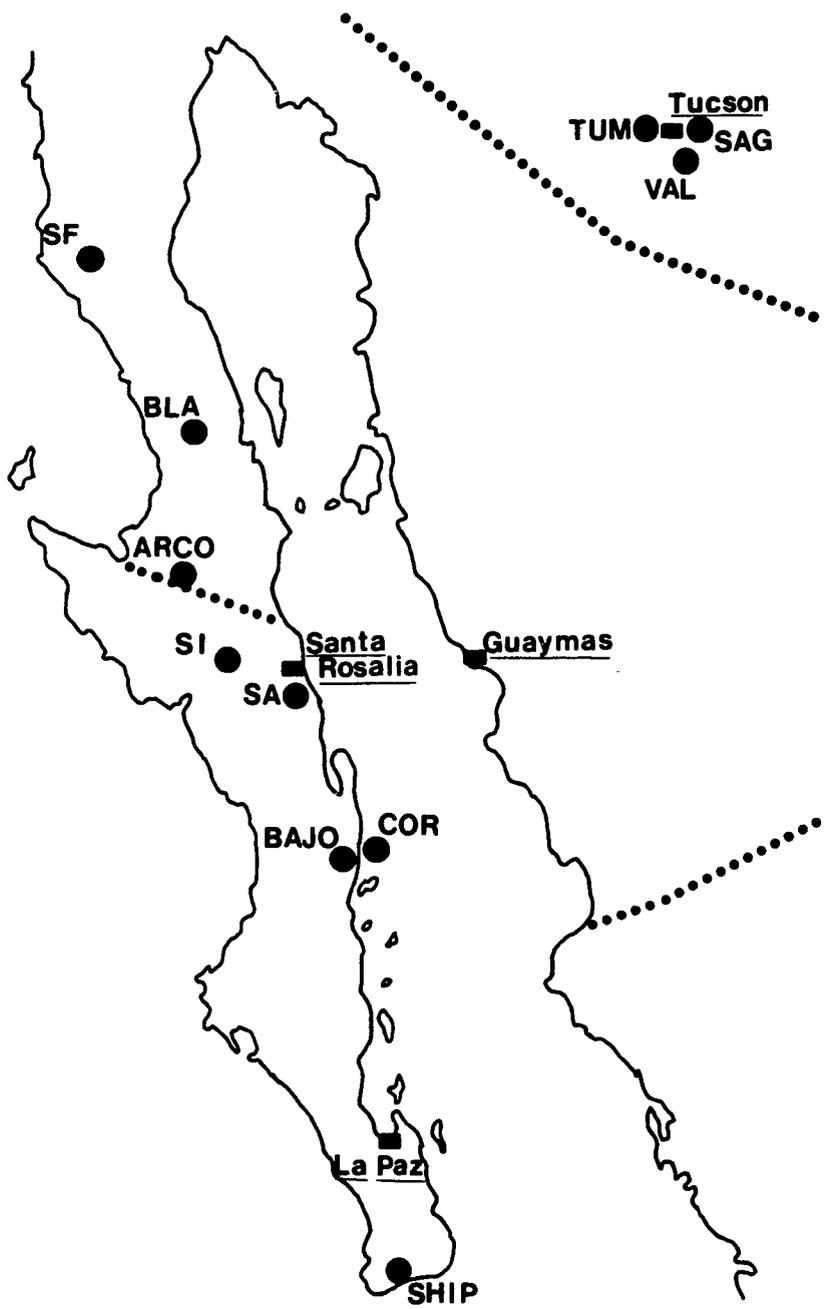


Figure 1. Map Showing Study Areas.

Table 1. Study Site Locations and Habitats.  
Terminology used largely follows Shreve (1951).

CODE:	LOCATION AND HABITATS SAMPLED
SF	San Fernando Velicata Mission Site, Baja California Norte. SFh -- hillside. SFw -- riparian thickets, <u>Prosopis juliflora</u> var. <u>Torreana</u> .
BLA	6 km E of Mex. Hwy. 1 on road to Bahia de los Angeles, Baja California Norte. BLA -- Bajada.
ARCO	10.6 km E of Mex. Hwy. 1 on Mex. Hwy. 16 to El Arco, Baja California Sur. ARCO -- plains/volcanic mesa.
SI	23 km E of San Ignacio on Mex. Hwy 1, Baja California Sur. SIp -- volcanic mesa. SIw -- dry wash (3 m wide). SIa -- small, dry barranca (500 m wide).
SA	1.2 km W of Mex. Hwy. 1 on road to Santa Agueda, Baja California Sur. SAh -- upper slope. SAw -- small, dry barranca (30 m wide, 48 m deep).
BAJO	10 km N of Loreto, Baja California Sur. BAJO -- dry wash (2 m) on lower bajada with coastal influences.
COR	SW side of Isla Coronado, 3 X 2 km island in Gulf of California, 10 km N/NE of Loreto, Baja California Sur. COR -- steep, sparsely vegetated, volcanic cobble slopes.
SHIP	6 km NE of Cabo San Lucas and S of Mex. Hwy. 1, Baja California Sur. SHIP -- lower bajada with coastal influences.
SAG	NW corner of Saguaro National Monument East, bordered on the N and W by Broadway Blvd. and Freeman Rd., Tucson, Arizona. SAGi -- interwash area of upper bajada. SAGw -- dry wash (3 m wide).
VAL	Bordered on the S and W by Valencia Rd. and Interstate 10, Tucson, Arizona. VALc -- cholla dominated plain of lower bajada. VALw -- dry wash (2 m wide).
TUM	NW base of Tumamoc Hill, bordered on the N and W by St. Mary's Rd. and Greasewood Rd., Tucson, Arizona. TUM -- dry wash (3 m wide) through upper bajada/ creosotebush ecotone.

Cape district is included in the Arid Tropical Region rather than the Sonoran desert (Shreve 1937), approximately half of the plant species are desert species from the north (Nelson 1921: 109).

The avifauna of the Cape, as of the rest of the peninsula, has overwhelming Sonoran, rather than tropical, affinities (Grinnell 1928, Stager 1960).

#### Nest Census Transects

Verdin and Cactus Wren nests were censused by walking a transect, usually 1 km in length, at each study site and recording information on the nest placement of both species. At one Arizona study site, nests were censused along a greater distance. Time constraints or abrupt habitat changes resulted in the sampling of shorter nest transects at four Baja California sites. (See Table 2.) The similarities between the nests of Verdins and Cactus Wrens allow them to be censused efficiently using the same "search image." Nests of both species are distinctive, conspicuous structures, and were visible at distances up to 50 m from the transects.

#### Cactus Wren Nests

Cactus Wren abundance was estimated by the number of nests per 1000 m transect of the habitat. Because of the dependence of Cactus Wrens on individual roosting nests, the

Table 2. Summary of Data By Study Site.

For each study site the following information is given: the lengths of the nest and vegetation transects sampled; the number of Cactus Wren nests per km of nest transect; the % Verdin nests built in cholla cacti; the sample size (N) of Verdin nests on which the previous figure is based; and the relative density of cholla cacti (% of the total density of Verdin nest plants). See Chapter 2 for details.

Site	Length Nest Transect (m)	Length Vegetation Transect (m)	Cactus Wren nests/km	% Verdin nests in cholla	N	Relative Density of Cholla
SFh	250	30	26.4	0	(0)	99.0
SFw	250	30	4	0	(6)	1.0
BLA	1000	150	8	93	(6)	36.5
ARCO	1000	150	2	75	(4)	55.8
SIp	1000	150	2	100	(2)	99.0
SIw	150	30	0	100	(1)	50.6
SIa	1000	150	4	100	(4)	52.2
SAh	1000	150	10	100	(4)	64.0
SAw	1000	150	0	25	(8)	0.1
BAJO	1000	120	1	30	(10)	29.3
COR	650	60	0	25	(8)	1.0
SHIP	1000	150	4	0	(6)	22.2
SAGi	1000	150	9	0	(6)	25.1
SAGw	1000	150	8	0	(0)	4.1
VALc	1000	150	18	0	(1)	99.4
VALw	1000	150	0	0	(11)	0
TUM	2500	210	0.8	58.3	(12)	10.6

number of structurally sound, habitable nests is an acceptable index of abundance (Anderson and Anderson 1973: 52, 156). The nests are large, conspicuous structures, 15-30 cm long. Censusing the nests, rather than the birds themselves, avoids the problem of temporal changes in the detectability of the birds.

Cactus Wren nests built for roosting or breeding show no essential differences and can be used interchangeably (Anderson and Anderson 1973: 22); therefore, no attempt was made to distinguish between types of nests for this analysis. Since young wrens may roost communally for a time after fledging, a count of nests during this period would tend to be a conservative estimate of population size (Anderson and Anderson 1973: 156).

#### Verdin Nests

For analysis of Verdin nest site selection, I enlarged my sample size by including data on old, "dilapidated" nests, i.e. those which had large holes or were caved in, but were positively identifiable as nests of Verdins. However, to avoid the chance of misidentification, I did not include nest "remnants," which I defined as nests missing major parts of the walls or roof. While some remnants can be confidently labeled as Verdin nests, identification becomes increasingly uncertain as the nests gradually deteriorate.

Verdin nests are built specifically for the purpose of breeding or for roosting. Roost nests built in the summer tend to

be small, simple, unlined structures readily distinguishable from breeding nests. However, autumn and winter roosts are large and substantially lined, and closely resemble breeding nests. The major structural differences between the two, according to Moore (1965) and Taylor (1971), are that breeding nests tend to have a larger cavity, deeper cup, and an entrance-way that forms a threshold or lip before the nest cavity. However, in examining active breeding nests I have found that nests vary and the above features are not an infallible key to a nest's function. Determining the original function of breeding nests of unknown age is therefore uncertain. The fact that old breeding nests and those from aborted breeding attempts may be used as roosts (Moore 1965) adds further complication. Data presented in this analysis of Verdin nest site selection includes both breeding and roosting nests.

#### Vegetation Transects

To determine nest plant availability, vegetational analysis of each study site was conducted by the line intercept method (Strong 1966). Plants at least 1 m tall were included in the analysis. At most sites data were collected along five 30 m transects which were located at intervals along, and parallel to, the nest census route in the following manner: the nest census kilometer was divided into 5 equal intervals of 200 m each and one 30 m vegetation transect was located randomly within each

interval. Due to time constraints, analysis was based on a lesser number of transects at five of the Baja California sites. At one Arizona site, seven transects were analyzed. (See Table 2.)

In my analysis, I considered as potential nest plants any species in which Verdin nests have been found by me or have been reported in the literature. I made two exceptions to this rule. First, I encountered along transects a few individuals of unidentified species of spinescent shrubs that were structurally very similar to typical Verdin nest plant species. Since Verdins are able to exploit a wide range of spiny shrubs in various desert habitats (e.g. Grinnell 1914, Taylor 1971), I assumed that these plants offered suitable nest sites for Verdins. In no case were any of these plants a dominant or important component of the vegetation.

Second, although Johnson et al. (1948) report finding a Verdin nest in creosotebush in the Mohave Desert, this species is not considered a Verdin nest plant in my analysis. The chromosomal race of creosotebush in the Mohave Desert is "bushier" and "more shrub-like" than the Sonoran or Chihuahuan Desert forms (Brown 1982b: 173) and therefore may be structurally more suitable as a nest plant. However, as discussed in the Introduction, in the Sonoran and Chihuahuan Deserts, creosotebush remains unused even when alternate nest sites are rare.

### Statistical Analysis

To examine the effect of Cactus Wrens on Verdin nest plant selection, the relationship of the following three variables was analyzed by partial correlation (Thorndike 1978): 1) the percentage of Verdin nests occurring in cholla; 2) the abundance of Cactus Wrens, as estimated from the censusing of nests; and 3) the availability of chollas as nest sites, expressed as the relative density of chollas versus other Verdin nest plants. Before statistical analysis, arcsine transformation was performed on percentages. (For a discussion of the use of arcsine transformation, see Sokal and Rohlf 1981.)

Even when nest plants occur in a habitat in only trace amounts, they can be very important as nest sites (Tomoff 1974). At 2 sites (COR, SFw) chollas are present in very low densities but were not intercepted by the plant transect line; to distinguish these from sites where chollas are absent, I arbitrarily assigned a relative nest plant density of 1% for cholla. In a case where only 1 or 2 individual plants of cholla were seen along the entire transect route (SAw), I assigned a relative density of 0.1%. Two cholla-dominated habitats with widely scattered trees (SIp, SFh), were assigned a relative density of 99% for cholla.

To examine the effect of Cactus Wrens on Verdin habitat use, the relationship of the following three variables was

analyzed by partial correlation: 1) number of Verdin nests per km; 2) number of Cactus Wren nests per km; and 3) percent vegetation cover of the habitat, a measure of vegetation density which distinguishes between wash habitats and more xeric habitats.

## CHAPTER 3

### RESULTS

The data from the nest and vegetation transects are summarized by study site in Table 2.

#### Verdin Nest Plant Selection and Cactus Wren Abundance

There is a weak, negative linear correlation between the percentage of Verdin nests in cholla and the abundance of Cactus Wrens. (See Fig. 2). This negative correlation is obscured, however, because each of these two variables is positively correlated to cholla density. Verdin nest plants include most of the common desert trees and thorny shrubs. The density of cholla relative to other Verdin nest plants is a measure of the local availability of cholla nest sites to Verdins as well as a fair predictor of the suitability of the habitat for Cactus Wrens, which favor areas where chollas are plentiful. Therefore, as the relative density of cholla increases, Verdins tend to make greater use of chollas as nest sites but the abundance of Cactus Wrens also tends to increase.

To better examine the association between Cactus Wren abundance and Verdin nest site selection, the effects of cholla density can be held constant statistically by partial correlation analysis (Thorndike 1978). Controlling for cholla density

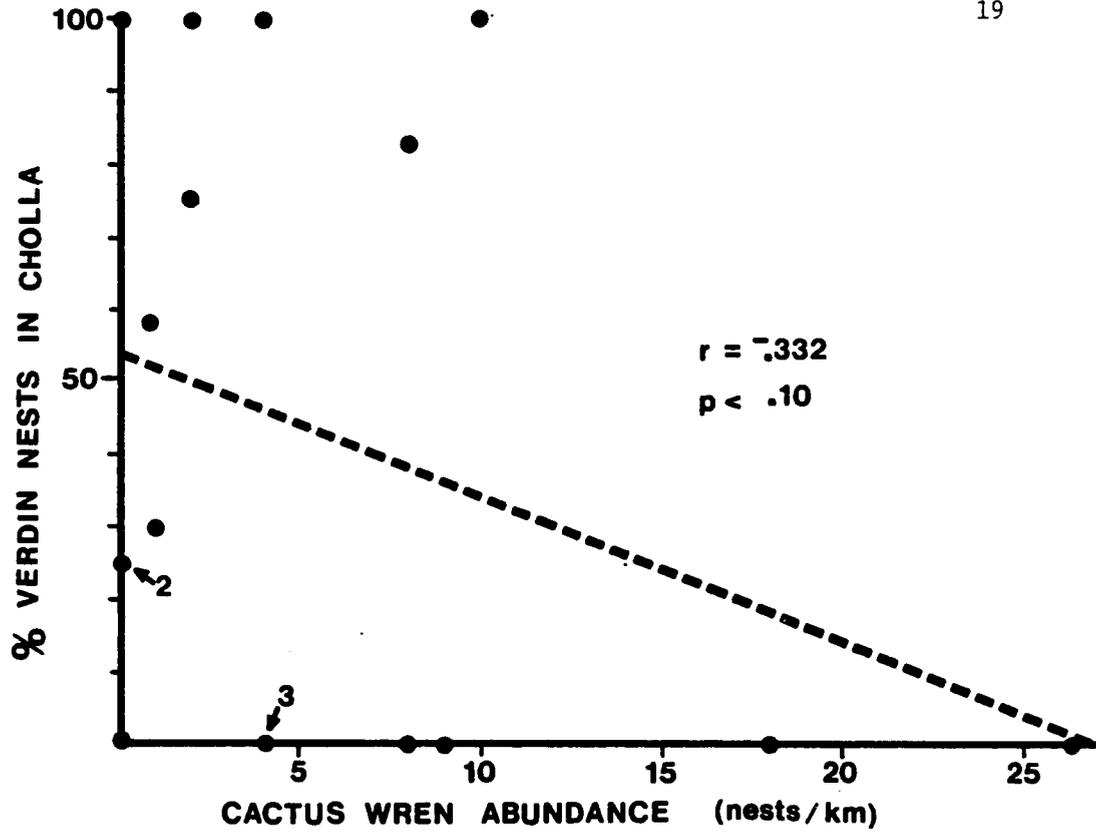


Figure 2. Verdin Use of Cholla Nest Sites as a Function of Cactus Wren Abundance.

Table 3. Results of Correlational Analysis of Verdin Nest Plant Selection.

Data collection and analysis is discussed in the text.

LINEAR CORRELATION COEFFICIENTS

	r	p
	-----	-----
Percentage of Verdin nests in cholla vs. Cactus Wren abundance	- .332	< .10
Percentage of Verdin nests in cholla vs. Relative nest plant density of cholla	.359	< .10
Cactus Wren abundance vs. Relative nest plant density of cholla	.597**	< .01

PARTIAL CORRELATION--CONTROLLING FOR CHOLLA DENSITY

	r	p
	-----	-----
Percentage of Verdin nests in cholla vs. Cactus Wren abundance	- .730**	< .005

(Table 3) reveals that there is a highly significant negative correlation between the percentage of Verdin nests in cholla and the local abundance of Cactus Wrens ( $r = -0.730$ ;  $p < 0.005$ ). Thus, at any given cholla density, the utilization of cholla nest sites by Verdins decreases with increasing numbers of Cactus Wrens.

#### Verdin Nest Plant Preferences

Examination of the the percentage of Verdin nests in cholla as a function of the cholla density demonstrates whether the nests occur in cholla in smaller or larger proportions than expected by its availability. As seen in Fig. 3, at 11 of the 14 sites where Verdins nested in the presence of cholla, they chose chollas as nest sites at a proportion at or above that expected by random selection among the potential nest plants (indicated by the dotted line:  $y = x$ ). This demonstrates that, despite the negative influence of Cactus Wrens, chollas represent a suitable, if not preferred, nest plant for Verdins.

#### Interspecific Segregation of the Nesting Habitats

The number of Verdin nests and the number of Cactus Wren nests in a habitat are negatively correlated (Fig. 4). Is this pattern of habitat segregation due to interspecific interference or is it simply a reflection of differing habitat requirements of the two species? Although there is considerable overlap in

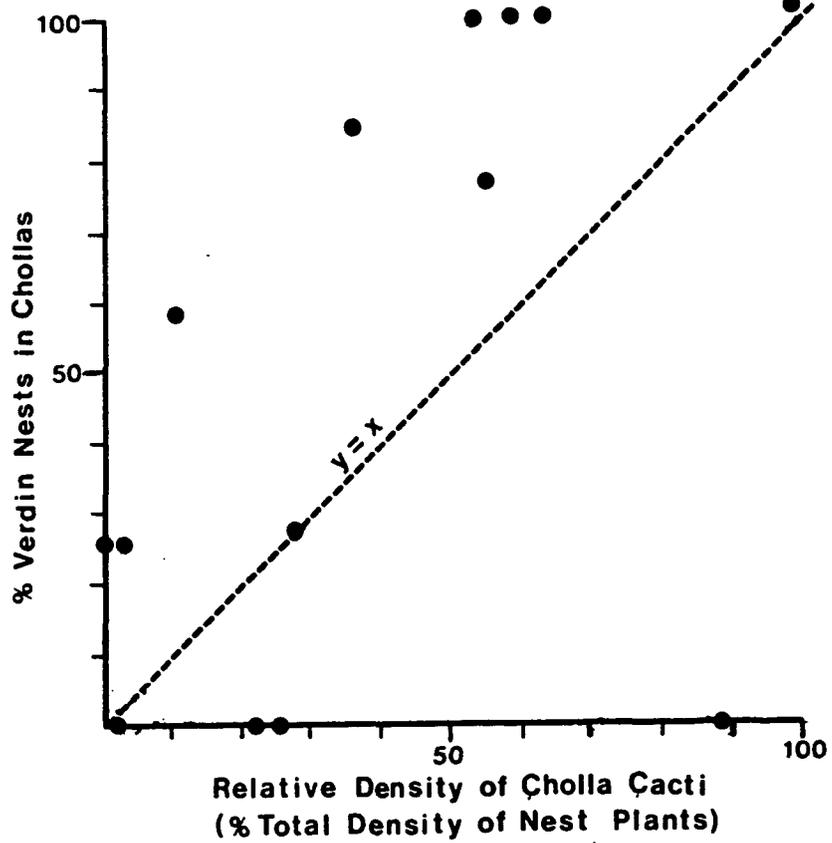


Figure 3. Verdin Use of Cholla Nest Sites as a Function of Nest Plant Availability.

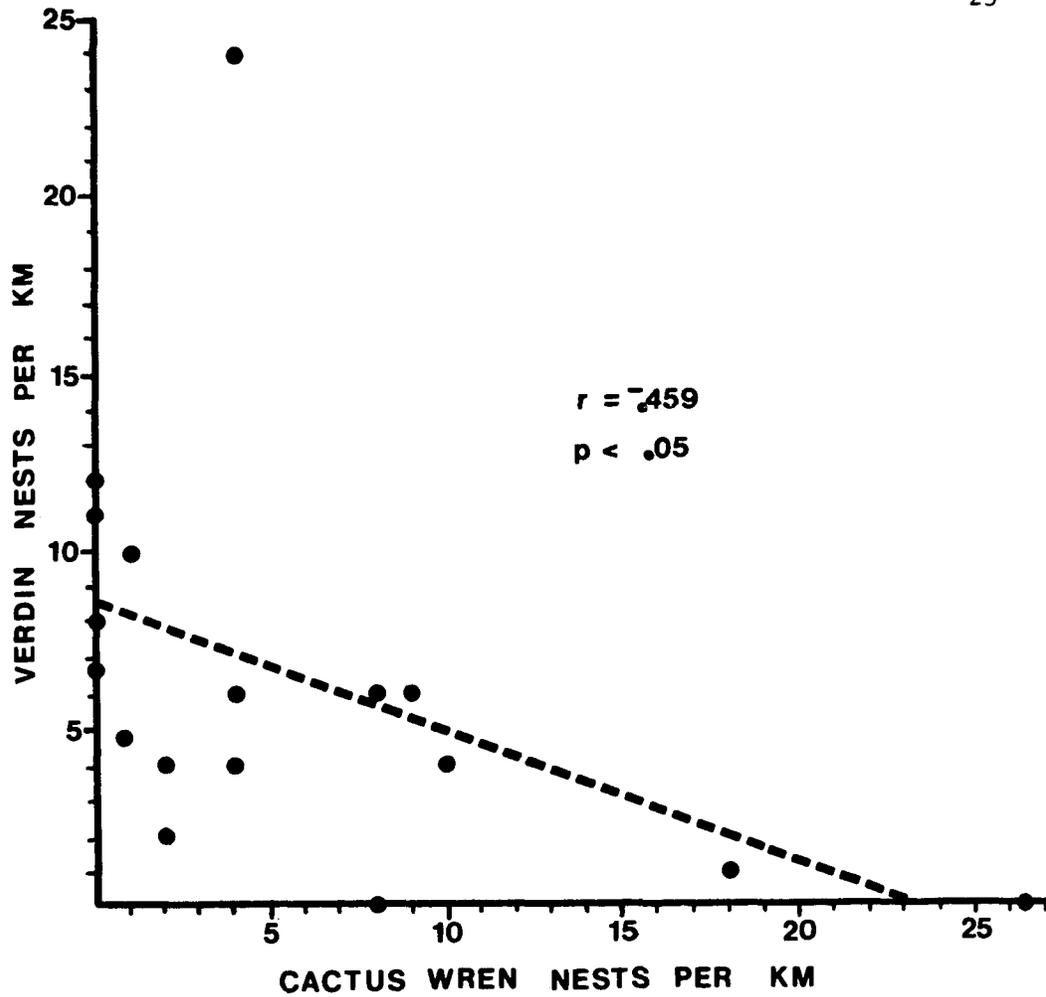


Figure 4. Verdin Nest Abundance as a Function of Cactus Wren Nest Abundance.

habitat utilization, Verdins typically nest in the denser vegetation along washes where there are few chollas while Cactus Wrens nest in adjacent open areas of high cholla density.

To determine the importance of habitat type in explaining nesting segregation, the vegetation density (percent cover) can be held constant statistically by partial correlation analysis (Table 4). Verdin nest abundance is positively correlated with vegetation cover, while Cactus Wren nests show a non-significant, negative correlation with vegetation cover. Controlling for vegetation cover only slightly weakens the negative correlation between the two species, from  $r = 0.459$  to  $r = 0.406$  (although this does increase the probability value above the .05 level of significance). These results suggest that only a small part of the pattern of nesting segregation among the study sites can be explained by the differential use of habitat types by the two species.

If nesting segregation reflects a response by Verdins to Cactus Wren interference, habitat use should diverge as Cactus Wren abundances increase. At five locations, study sites included a wash habitat as well as a more xeric, adjacent habitat. With the exception of one site, the proportion of Verdins nesting in the wash habitat increases with Cactus Wren abundance (Fig 5-a). As illustrated in Fig. 5-a and 5-b, Cactus Wrens often nest only in the habitats away from the wash;

Table 4. Results of Correlational Analysis of Habitat Segregation.

Data collection and analysis is discussed in the text.

<u>LINEAR CORRELATION COEFFICIENTS</u>		
	<u>r</u>	<u>p</u>
Verdin nests per km vs. Cactus Wren nests per km	- .459*	< .05
Verdin nests per km vs. Percent vegetation cover	.411*	= .05
Cactus Wren nests per km vs. Percent vegetation cover	- .246	< .25
<u>PARTIAL CORRELATION--CONTROLLING FOR PERCENT VEGETATION COVER</u>		
	<u>r</u>	<u>p</u>
Verdin nests per km vs. Cactus Wren nests per km	- .406	< .10

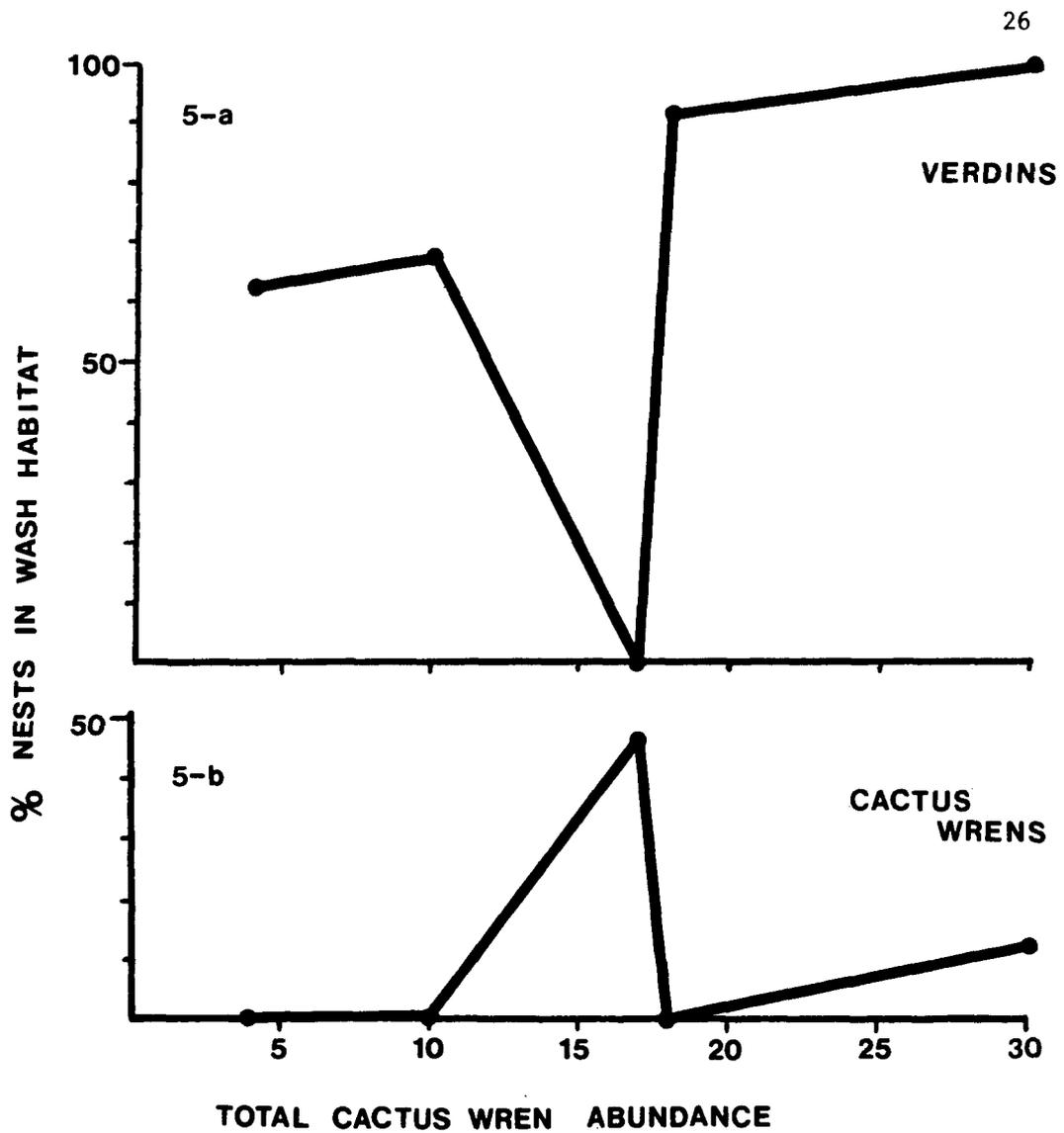


Figure 5. Verdin and Cactus Wren Use of Wash Habitats as a Function of Cactus Wren Abundance.

however, at the anomalous site where Verdins are completely absent from the wash habitat, Cactus Wrens are unusually abundant in the wash. At this site the Cactus Wrens nest in both habitats, mostly in chollas, while the Verdins nest away from the wash in palo verde trees (Cercidium microphyllum). This pattern, although atypical, is consistent with the hypothesis that Verdins are avoiding the use of nest sites favored by Cactus Wrens.

## CHAPTER 4

### DISCUSSION

Cactus Wren aggressive interference with Verdin nesting may derive from a combination of several phenomena governing Cactus Wren behavior: the importance of cholla cacti as preferred nest sites, the importance of enclosed nests, and the behavioral predisposition of wrens (Troglodytidae). As will be discussed below, both the nest itself and the nest plant are valuable resources with the potential to become the focus of competitive interactions. In addition, many members of the wren family share a number of similar interspecific interference behaviors involving the disruption of nests. Do such behaviors have any adaptive significance? I will address the question of whether interference behaviors represent an adaptive response to competition over limited resources and discuss other possible selective advantages which could favor nest interference.

#### Interspecific Competition for Cholla Nest Sites

Arborescent cholla cacti are used extensively for nest sites by many species of birds in the Sonoran Desert. Several species, such as the Cactus Wren, Curve-billed Thrasher (Toxostoma curvirostre), House Finch (Carpodacus mexicanus) and Roadrunner (Geococcyx californianus), exhibit a conspicuous preference for cholla nest sites. Other desert species which

also nest in chollas include the Verdin, LeConte's Thrasher (Toxostoma lecontei), Bendire's Thrasher (Toxostoma bendirei), Mockingbird (Mimus polyglottos), Brown Towhee (Pipilo fuscus), Black-throated Sparrow, Rufous-winged Sparrow (Aimophila carpalis), White-winged Dove (Zenaida asiatica), Mourning Dove (Zenaida macroura), and Inca Dove (Scardafella inca).

Recognition of the importance of cholla cacti as nest sites in the Sonoran Desert has stimulated discussions of the possible advantages of using cholla and of the potential for interspecific competition over favored cholla sites.

#### Advantages of Nesting in Cholla Cacti

Cholla cacti have extremely sharp, barbed spines which easily penetrate skin. These spines presumably act as a deterrent to nest predators, as they are certainly a deterrent to ornithologists studying cholla nesting birds (Anderson and Anderson 1973: 83; Miller, 1936; innumerable personal observations). The spines are a danger even to cholla nesting species. Young of Cactus Wrens, Curve-billed Thrashers, and Verdins as well as House Sparrows (Passer domesticus) have been found impaled on cholla spines (Miller 1936; Anderson and Anderson 1973; Jaeger 1922: 73; Bent 1948: 392; Hensley 1954). Anderson and Anderson (1973) found that House Sparrows avoid chollas and would not land on one even if enticed with food. Some cholla nesting birds will, when building the nest, clip the spines off

the joints to be used as the immediate nest site (Phillips, Marshall and Monson 1964: 113; Bent 1948: 392; Johnson et al. 1948).

The above observations suggest that there is some benefit of nesting in cholla which offsets the hazards of navigating through the spines and give credence to the intuitive explanation that the spines act as fortification against nest predators. There have, however, been few comparative studies of the breeding success or the predation rate of nests built in cholla versus in other plants. Anderson and Anderson (1973: 146) present data on nest predation for Cactus Wren breeding nests observed at one site over 5 years. 95% of all the nests (142/154) were placed in chollas or saguaros. Of these, 40% of the saguaro nests were lost to predation compared to 26% of the cholla nests. Based on a small sample of 45 White-winged Dove nests, Arnold (1943: 31) states that the percentage of successful nests was greatest for nests built in low, open sites in cholla.

From what kinds of predators would nests built in cholla be protected? Racers (Coluber), coachwhips (Masticophis) and gopher snakes (Pituophis), which are important nest predators, can climb chollas (Jaeger 1922, 1950; Anderson and Anderson 1973: 194); nevertheless, cholla nest sites may confer relatively greater protection than shrubs (Brandt 1951: 172-179).

Roadrunners, which nest in chollas, would not be deterred. Round-tailed Ground squirrels (Citellus tereticaudus), Harris' Antelope Squirrels (Ammospermophilus harrisi), and White-throated Woodrats (Neotoma albigula) also climb chollas but there seems to be no evidence that these rodents are nest predators (Arnold 1943: 13, 24; Vorhies and Taylor 1940, Anderson and Anderson 1973). Cholla does offer protection against domestic cats (Bent 1968: 321; Brandt 1951: 180) and probably functions similarly as a defense against native mammals such as coyotes, skunks, bobcats, ring-tails and foxes; as well as predaceous birds such as hawks, owls, ravens and shrikes. Vorhies and Taylor (1940) came to a similar conclusion regarding the protective function of cholla joints overlaying the dens of White-throated Woodrats (N. a. albigula). The dens are constructed preferentially under chollas, and cholla joints are collected from great distances and arranged by the rats to fortify the den and runways.

Nesting in chollas may be advantageous for reasons other than predator protection. Ohmart (1973) attributed the preference of the Roadrunner for cholla primarily to the branching structure which allows the nest to receive direct sunlight for solar brooding but also provides bands of shade during the extreme heat of the day. He suggested that predator deterrence and nest support are possible secondary benefits of cholla sites. However, shading is less likely to be a critical factor in the

choice of chollas in such species as Cactus Wrens, Verdins, and the doves, which usually nest on the exposed periphery of the cactus.

#### Competition Among Cholla Nesting Species

The conspicuous preference shown by a number of birds for nesting in cholla has motivated several previous discussions on the possibility of interspecific competition for cholla nest sites. The Curve-billed Thrasher, also a year-round resident, shares with the Cactus Wren a close association with cholla cactus. The nests of Curve-billed Thrashers are bulky stick structures often placed in the interior portion of a cholla so that they are quite effectively surrounded by cholla joints. During breeding, eggs are laid in a finely lined cup within the stick structure. During the nonbreeding season the thrashers roost in chollas, often on the nest structure or on other small platforms of sticks (Anderson and Anderson 1973: 171; Bent 1948: 397). Relined nest structures may be used for several clutches and for successive years (Anderson and Anderson 1973: 181).

Emlen (1974) suggested that Curve-billed Thrashers and Cactus Wrens may compete over the few chollas remaining in residential areas. Huey (1942) and Hensley (1954) felt that, in desert habitats, Curve-billed Thrashers exclude Cactus Wrens from building in the best cholla nest sites. Anderson and Anderson (1973), documenting extensive interference of Cactus

Wren nests by Curve-billed Thrashers, reported that the unattended roost nests of the wrens are often torn to pieces by the thrashers. Anderson and Anderson (1973) argued, however, that since there appears to be a surplus of suitable chollas, and since thrashers do not generally build at the site of the destroyed wren nests, nest site competition is not an important factor in the thrasher behavior. They concluded that there was no evidence that interference by thrashers in cholla is influencing the nest site selection of the wrens either by forcing the wrens to nest in inferior chollas or in plants other than cholla. They apparently did believe, however, that interspecific interference could influence nest site selection of House Finches in cholla and suggested that the finches "chose only the sites which the wrens permitted them to have."

Although they documented about 200 incidents of nest destruction by thrashers and described the behavior involved as having a stereotyped and deliberate pattern, Anderson and Anderson (1973) dismissed this interference as having little importance since the active breeding nests of the wrens are "spared." However, the use of the word "spared" is certainly misleading. The most evident reason that breeding nests containing eggs or young are not destroyed is that they are the only types of nests which the Cactus Wrens actively defend. Like roost nests, breeding nests that are under construction and those from

which the young have fledged (but in which they may still roost for several months) are subject to attack from thrashers. Anderson and Anderson (1973) themselves stressed that Cactus Wrens do not built superfluous "decoy" or "dummy" nests; all nests built are of value. Nests are used by the adults immediately as roosts, and/or later converted into breeding nests, or they may provide roosts for the young before the immature birds disperse (Anderson and Anderson 1973). I am skeptical, therefore, of the conclusion that the repeated destruction of nests, which take over a week to complete, can be considered a negligible detriment to Cactus Wrens.

While it is quite possible that in some habitats a shortage of suitable cholla nest sites would intensify aggressive interactions among cholla nesting species, I am not arguing here that competition over limited cholla nest sites is the driving force behind Cactus Wren interference with Verdin nesting. Species of birds nesting in chollas are likely to have frequent encounters. I propose that Verdins nesting in chollas rather than in shrubs are increasing their encounter rate with Cactus Wrens and thereby significantly increasing the probability that their nests will become the target of Cactus Wren interference.

How do birds develop preferences for particular types of nest sites? Nest site preference appears to be a labile trait molded by a combination of innate tendencies, imprinting and

learning. Some young birds imprint on the natal type of nest site (Temple 1978, Sargent 1965). In Zebra Finches (Poephila guttata) the imprinting process is more important in the fledgling rather than the nestling period (Sargent 1965). Verdin fledglings gain considerable experience with the natal nest site due to a prolonged period of parental care and communal roosting behavior. Also, Verdins sometimes "copy" nest site selection by building a new nest over the remains of an old one (Moore 1965). Birds can learn by experience to avoid unsuccessful nest sites and to switch to a new type of site after a nest has been disturbed by predators (Humphrey and Peterson 1978, Robinson 1983). By combining learned behaviors with culturally (or even genetically) inherited tendencies, preferences for locally successful types of sites could be maintained, yet nest site preferences could respond readily in an environment in which the selective forces determining nest success varied temporally or spatially. (See also Temple 1978.)

In summary, interspecific nest interference among cholla nesting birds is well documented but the causal role of competition over nest sites remains debatable. The results of this study provide evidence that in one cholla nesting species, the Verdin, such interference can alter local patterns of nest site selection. Below, I will further discuss whether these interference behaviors have any adaptive significance.

### Interspecific Competition for Enclosed Nests

Enclosed nests are analogous to cavity nests in many ways. Collias and Collias (1984: 28) suggest that widespread building of enclosed nests in the tropics may have evolved as a substitute for tree holes. Skutch (1976) elaborates on two otherwise rare aspects of nest usage which are common to both cavities and enclosed nests: the use of nests as "dormitories" or roosts and the use of nests by "secondary tenants" of a species other than the original builder.

#### Advantages of Breeding and Roosting in Enclosed Nests

The building of enclosed nests which also function as year-round roosts is well known among many wrens, weaverfinches (Ploceidae), spinetails and thornbirds (Furnariidae), mannikins (Estrildidae), and flatbills (Tyrannidae), as well as individual members of other families. The construction of these nests often requires a considerable investment of time and energy; they may take from several days to many months to build and are very often sturdy, persistent structures. Many of the above species live communally or colonially, which allows for the more efficient building and defense of large and elaborate enclosed nests. Possible advantages of breeding and/or roosting in an enclosed nest are like those of cavity nesting and include protection from predation and insulation from harsh environmental conditions.

Predation appears to be by far the major cause of nesting mortality in most birds (Ricklefs 1969, Skutch 1966, Cody 1971) and is believed to have been a major evolutionary force in determining nest form and structure (Collias and Collias 1984: 142). Cavity nests have the lowest predation rates but are often the focus of fierce competition. The widespread evolution of enclosed nests in tropical birds is probably a reflection of the higher rate of nest predation combined with intense competition for cavities in the tropics (Collias and Collias 1984: 28; Skutch 1976: 436). The proportion of enclosed, versus open or cavity, nests is at least 2-3 times greater among the birds of tropical versus temperate regions (Collias and Collias 1984: 28).

Enclosed nests are safer than open nests; they generally have predation rates that are intermediate between those of open nests and cavities (Nice 1957, Oniki 1979, Loiselle and Hoppes 1983) and show correspondingly intermediate incubation rates, nestling periods, and clutch sizes (Lack 1968: 172). In addition to concealing the nest contents, enclosed nests often incorporate additional devices which may deter arboreal and/or terrestrial predators, e.g. having a pendulous structure, small ventral entrances, long entrance tubes, or an armor of thorny twigs placed over the nest and surrounding branches. Also, the nest may be placed in inaccessible locations such as the distal

ends of branches or over water, or may be associated with noxious plants or insect colonies.

Environmental stresses which may be attenuated in the microhabitat of an enclosed nest include extreme solar radiation (both ultraviolet radiation and heat load), excessive precipitation, low winter or nocturnal temperatures, low relative humidity, and chilling or desiccating winds. The direction of the nest entrance may be oriented in relation to the prevailing winds (Ricklefs and Hainsworth 1969; Austin 1974, 1976). Reduced energetic requirements may allow a species to breed or overwinter in inhospitable climates (Skutch 1976, 397-398; Goldstein 1974). Since the brood is not left directly exposed to predators or to the elements, enclosed nests reduce the risks of leaving the nest unattended and free time for the parents to engage in foraging and other activities (Lack 1968: 172).

#### Secondary Use of Enclosed Nests

It is widely accepted that nesting cavities represent a critical resource for some birds and may become the focus of competitive interactions (e.g. Lack 1954, Ricklefs 1969, Snyder 1978, Collias and Collias 1984: 14, 126-128). The same is true of enclosed nests. Numerous species of birds will opportunistically use for roosting and/or breeding an enclosed nest of a different species (Skutch 1976). While many secondary tenants use nests which have been previously abandoned, others are known to,

at least on occasion, forcibly evict the original occupants (Skutch 1976, Collias and Collias 1984: 131-132). Some populations and species have become specialists at usurping nests and breed exclusively in enclosed nests which they appropriate aggressively from another species (Skutch 1976).

In summary, to certain birds enclosed nests, like cavities, are a valuable resource which plays an important role in the life history of the species and requires a considerable investment of time and energy to build. Because they are useful to secondary tenants and susceptible to theft by more aggressive birds, it is not surprising that enclosed nests can become, as cavities do, the focus of interspecific competition.

Individual, enclosed roosting nests are important to both Verdins (Moore 1965, Taylor 1971) and Cactus Wrens (Anderson and Anderson 1973). In both species, birds will opportunistically make use of nests they did not build. For example, Moore (1965) found that 1/3 of the Verdin nests on his study site were used successively by two or more individuals; one nest, already old, was used by 5 different Verdins. Cactus Wrens also roost in any habitable nest available (Anderson and Anderson 1973).

Not surprisingly, secondary use of Cactus Wren and Verdin nests for breeding or roosting has been reported for a number of other species including Ash-throated Flycatchers, Myiarchus cinerascens (Finch 1982), House Sparrows (Anderson and Anderson

1973: 189); and Verdins (Taylor 1971) in Cactus Wren nests; and Bewick's Wrens, Thyromanes bewickii (Moore 1965), and Lucy's Warblers, Vermivora luciae (Gilman 1909, Brandt 1951: 79) in Verdin nests. I observed a pair of Lucy's Warblers repeatedly carry nest material into a newly constructed Verdin breeding nest until the Verdin chased them away. House Sparrows are able to usurp Verdin nests, and Taylor (1971) suggested that this may limit the success of Verdins in residential areas. Cactus Wrens not only roost in empty Verdin nests but, as discussed above, are able to usurp occupied Verdin nests.

From the above discussion, it is apparent that the enclosed nests of Verdins are a valuable resource, the possession of which they must defend against individuals of other species, as well as other Verdins. Due to the great similarities in nest usage and structure as well as nesting habitat, conflicts with the aggressively dominant Cactus Wrens are likely to be the most important of these interspecific interactions.

#### Interspecific Interference Behaviors of Wrens

As suggested by Picman (1980), nest and egg destruction and related intraspecific and interspecific interference behaviors seem to be a common feature of the wren family (Troglodytidae). Destruction of nests has been observed in the House Wren (Troglodytes aedon), Marsh Wren (Cistothorus palustris), Sedge Wren (C. platensis), and Bewick's Wren, as

well as the Cactus Wren (Picman 1980, and references cited therein). Predation for food is not a important factor in the destruction of eggs and nestlings by wrens. Wrens will remove nest lining material, fill nest cavities with twigs, puncture and/or toss eggs from nests, and peck young nestlings to death. The contents of the egg are only very rarely eaten. Damaged eggs and dead nestlings will often be carried out of the nest by the wrens and dropped (Sherman 1925a, b; Swank 1927; Picman 1977, 1980).

House Wrens have long been infamous for their depredations on the nests, eggs, and nestlings of other species (Sherman 1925a, 1925b; Swank 1927; Bent 1948). One study examined the effects of House Wrens on Prothonotary Warblers (Protonotaria citrea), both cavity nesters. When nesting sympatrically, the House Wren reduces the fledgling success of the warbler over 50% by puncturing the warblers' eggs (Walkinshaw 1941). Although the majority of species with which the House Wren interferes are cavity nesters, many species which build open nests also suffer losses.

Recently Picman (1977, 1980, 1981) documented that behaviors involving interspecific nest and egg destruction, especially against Red-winged Blackbirds (Agelaius phoeniceus), are highly developed in the Marsh Wren. The smaller and more maneuverable wrens approach and destroy blackbird nests in dense vegetation

However, in more open vegetation, the blackbirds can protect their nests and otherwise interfere with the wrens by chasing them (Picman 1980, 1981). Each species nests where it can best reduce the aggressive impact of the other, which results in interspecific territoriality and habitat segregation along a density gradient of marsh vegetation. (See also Orians and Willson 1964.)

There is evidence that Cactus Wrens possess the full range of interspecific interference behaviors that have been documented in other wrens. Anderson and Anderson (1973: 189-192) describe Cactus Wrens removing and breaking eggs, removing nest material, and probably killing a nestling from nests of House Finches and House Sparrows. As in the other wrens, this behavior does not seem to be based on predation for food. As discussed in the Introduction, disruption of Verdin nests by Cactus Wrens is well documented. House Sparrows, Black-tailed Gnatcatchers (Polioptila melanura) (Anderson and Anderson 1973) and Verdins (Taylor 1971, personal observations) all mob Cactus Wrens which approach their nests. The question of whether nest interference by Cactus Wrens is infrequent and opportunistic or whether it involves a more highly developed behavior pattern, such as is seen in the House and Marsh Wrens, is worthy of closer examination.

### Interference Versus Exploitative Competition

Traditionally it has been assumed that exploitative and interference competition both result from a condition of limited resources and produce similar effects. For example, Case and Gilpin (1974) in a discussion of the mechanism of interference competition state, "Interference competition works by freeing resources for the interfering population. Obviously, a population that interferes against a population that is not a resource competitor pays a cost that returns nothing. Such interference will not evolve." However, as Maurer (1984) has pointed out, the assumption that resource limitation is critical for interspecific competition to occur is based (often implicitly) on a specific mathematical model of competition, the Lotka-Volterra model.

Maurer (1984) suggested that under conditions of abundant resources, although exploitative competition would be relaxed, interference might intensify if the density and dispersion patterns of the resource resulted in an increased encounter rate between individuals of the species involved. The results of this study support this prediction; in areas of high Cactus Wrens densities, Verdins are avoiding the use of cholla nest sites even though the cholla may be very abundant. It is not necessary to invoke resource limitation to maintain either that interference by Cactus Wrens can prevent Verdins from utilizing cholla nest

sites or that interference is an adaptive behavior on the part of the wrens.

As Case and Gilpin (1974) point out, the development of interspecific interference behaviors by a species may be favored by preadaptations involving intraspecific interference. Cactus Wrens opportunistically make use of roosting nests built by other individuals. Fledgling and juvenile birds especially depend on the availability of nests long before they start to build nests themselves. The communal roosting of juveniles ends as antagonism increases among them; eventually, the most aggressive individual retains possession of the nest while the rest must find other sleeping quarters (Anderson and Anderson 1973). Adult birds whose nests are suddenly destroyed or appropriated by other individuals, also seek out unused, nearby nests in which to roost. The obvious advantage of being aware of such potential roosting places would favor inquisitive behavior by Cactus Wrens towards cholla cacti and towards all Cactus Wren nests encountered. Such behavior could easily be transferred to the similar enclosed nests of Verdins.

Interference will be most effective when costs are low and benefits are high (Case and Gilpin 1974). Yet, even if benefits are small or infrequent, interference behavior will be favored as long as the benefits outweigh the costs. The usurping of nests by Cactus Wrens seems to be primarily an opportunistic

behavior which offers to the wrens occasional, significant benefits at little or no cost. As such, it may have only slight selective value to the wrens, independent of the advantages of similar intraspecific interference behaviors. However, the interactions between Cactus Wrens and Verdins are not symmetrical. In an area where harassment by Cactus Wrens occurs frequently, there should be considerable selection for Verdins to minimize these confrontations by avoiding the nests sites (chollas) and the nesting habitats (such as open cholla flats) most preferred by the wrens. Thus this conflict may result in the divergence in resource utilization of a resource (cholla nest sites) which is not in limited supply.

This divergence in use of nest plants agrees with the prediction of Case and Gilpin (1974) that unidirectional interference between resource competitors will lead to abutting distributions, with only the subordinate species restricting its niche. In the present study, the mutually utilized resource in question may be either the nest plant, or the enclosed nest itself. In neither case, however, is the conflict necessarily a case of resource competition. At least where chollas are abundant, neither species is depriving the other of a resource by their mutual use of the same kind of nest plant. If we consider the enclosed nest as the resource, then Cactus Wrens, by stealing Verdin nests, are acting not as competitors but as facultative

social parasites. The negative effects of this interaction are not mutual; the Verdins are having a positive effect on the wrens by providing potential roosts. Similarly, in obligate secondary nesters that usurp nests, such as species that usurp the cavities made by woodpeckers, interference is a parasitic rather than competitive interaction.

Interference and Indirect Species Interactions:  
Density-Dependent Nest Predation

As I have discussed above, certain conditions in which there is a limited supply of nest sites or nests may result in conflicts between cholla nesting species. However, why would interference behaviors evolve or be maintained in situations where neither nests, nest plants, nor food are contested resources? Fretwell (1972) proposed that birds are limited during the breeding season by nest predation, and that since the "search image" developed by predators for nests of one species aids in finding the similar nests of other species, predation increases with the total nest density for all species. As a result there is selective pressure for species to diverge in the form and placement of their nests. Ricklefs (1969) attributes the greater diversity of nest types in tropical oscines to specializations against various groups of predators and also suggests that the increased diversity of nests decreases the efficiency of a predator's search image. Tinbergen, Impeken,

and Franck (1967) and Alcock (1975) propose similarly that the searching behavior of predators can exert selective pressure for prey species, particularly the vulnerable eggs and young of birds, to maintain a widely spaced distribution. The manipulative field studies of Tinbergen et al. (1967) support this idea. It follows from these arguments that there may be selection for interspecific aggression in order to decrease the overall density of nesting birds, especially of birds nesting in similar nest sites, and thereby decrease predation rates.

This offers an alternate hypothesis explaining the evolution of interspecific aggression among cholla nesting birds that does not directly involve competition over nests, nest sites, food, or any other mutual resource. Even without competing directly, species nesting in chollas could have an indirect negative effect on one another by each having a positive effect on their mutual predators. In this case, therefore, contrary to the conclusion of Case and Gilpin (1974), natural selection could favor the evolution of interference between species which are not resource competitors.

Unless nest destruction can exclude other birds from even foraging in the area, it would be ineffective in preventing competition for food. Especially in a case where the species doing the interfering is larger in size, one would expect interference based on food competition to consist primarily of direct

aggression, rather than nest disruption, to maintain interspecific territoriality (Orians and Willson 1964). If limited nests or nest sites are the basis of the interference, one would expect to see individuals of the interfering species usurping nest sites from the species whose nests they disrupt. However, if breeding or roosting nests are the focus of the search behavior of a mutual predator, destruction of similar neighboring nests, rather than direct aggression, might be the most cost effective way for a bird to maintain in its territory a low overall density of prey apt to attract its predators.

The nests of Cactus Wrens, being enclosed and peripherally placed, closely resemble the nests of Verdins in form and placement. By utilizing primarily chollas and occasionally trees, Cactus Wrens overlap greatly in nest plant selection with Curve-billed Thrashers but also considerably with Verdins. Thus, aspects of the nesting behavior of the wrens closely resemble both species with which it is involved in frequent nest interference interactions. The persistent destruction of Cactus Wren nests by Curve-billed Thrashers, which perplexed Anderson and Anderson (1973), seems to fit the hypothesis that interspecific nest destruction is a selective response countering the searching behavior of nest predators. Both species roost as well as breed in chollas. There appears to be an abundant supply of cholla nest sites and little competition between the two species over

food, yet the larger thrashers exhibit a stereotyped interference behavior of tearing apart nests of the wrens.

The case of Cactus Wrens interfering with Verdins in cholla is more complex. Cactus Wrens are known to interfere by usurping Verdin nests as roosts as well as by simply destroying nests. Since the enclosed nest of the Verdin is a resource of potential value to the wrens, this destructive behavior seems maladaptive. This latter component of the wren interference behavior may reflect a conflict between selective pressures which favor the use of roosts but act against maintenance of high nest densities which may attract predators.

The few experimental tests of Fretwell's hypothesis, that predation rate increases with nest density, have yielded conflicting results. Possible confounding factors include anti-predator aggression, which may be more effective under high nest densities, and differences in the types of nest predators considered (e.g. Goransson et al. 1975, Gottfried and Thompson 1978). Studies of search image formation generally involve visually oriented predators (e.g. birds) and may not be applicable when snakes are the most important nest predators. Thus, further investigation is needed on the relationship between nest density and predation risk before we can assess the role of this interaction on the evolution of interspecific nest interference behaviors.

## CHAPTER 5

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