

tolerance of floaters by breeders allows them access to the best habitats. Floaters appear to be as dependent on cached acorns as breeders and may be closely tied to these stores during the winter. Floaters may spend fall and winter in areas of high acorn production, despite the fact that these areas provide relatively few breeding opportunities. In the spring, near continuous distribution of oak woodland provides lepidopteran larvae and other insects over a wide area. Floaters are then free to move regionally and search out breeding areas, particularly in areas of prior acorn crop failures that may offer more territory vacancies. This pattern of food abundance may also contribute to the tolerance of floaters in the winter (when acorns are superabundant) and intolerance in the breeding season (when insect prey is important and starvation rates of nestlings are high).

Key words: *Aphelocoma*, acorn production, cooperative breeding, dispersal, floating, scrub-jay, social behavior.

INTRODUCTION

Long-term field studies have contributed greatly to our knowledge of the demographic and ecological factors that promote delayed dispersal, larger group size, and increased cooperation in cooperatively breeding birds. Theories based on these studies differ in stressing the relative importance of various demographic and ecological factors both in the maintenance of cooperative breeding and in modeling the evolution of group living and cooperative breeding from an earlier noncooperative state. Similar long-term studies of appropriate noncooperative species are essential for the comparisons required to test these theories and their underlying assumptions. The Western Scrub-Jay (*Aphelocoma californica*) and other species in the genus provide a unique and unparalleled opportunity to make such comparisons. *Aphelocoma* jays are similar in morphology and general aspects of behavior, their social organization ranges from the noncooperative Western Scrub-Jay to the plural-breeding, cooperative Mexican Jay (*A. ultramarina*), and there is a wealth of information on two cooperative members of the genus, the Mexican Jay and the Florida Scrub-Jay (*A. coerulescens*).

APHELOCOMA JAYS

Nearly all races of scrub-jays in western North America breed noncooperatively. Young disperse from their natal territories soon after becoming independent and then, over the ensuing months, attempt to acquire territories and breeding status. Despite their wide geographic range and the diversity of habitats used, only one population (*A. californica sumichrasti*) in the mountains of southeastern Mexico is known to live in family groups (Burt and Peterson 1993).

The insular Island Scrub-Jay (*Aphelocoma insularis*) has been the best studied western population (Atwood 1980a,b; Atwood et al. 1990); it became isolated from the mainland population during the Pleistocene (Pitelka 1951), almost certainly after the western populations had lost traits of cooperative breeding (see below). In contrast to the noncooperative Western Scrub-Jays, the cooperatively breeding Florida Scrub-Jay (Wolfenden 1974, 1975; Wolfenden and Fitzpatrick 1977, 1978, 1984, 1986, 1990; Fitzpatrick and Wolfenden 1986, 1988; Mumme 1992) and Mexican Jay (Brown 1963, 1970, 1974, 1994; Brown and Brown 1981a, 1984, 1990; Brown et al. 1997; Trail et al. 1981) have been intensively studied for 25+ years. In Florida Scrub-Jays, offspring from a single breeding pair may delay dispersal for one to several years, forego breeding, and help in defending the territory and raising offspring in subsequent breeding efforts. Roughly one-half of all pairs have helpers in any given year. The Mexican Jay exhibits geographic variation in group size and social behavior (Strahl and Brown 1987, Brown and Horvath 1989) ranging from singular breeding (one breeding female per group) to

up to five breeding pairs on a single group territory. Offspring may delay dispersal and breeding for up to six years and help; some offspring never disperse but become breeders on their natal territories. Both nonbreeders and breeders participate in territory defense and care for young at all group nests. Less is known of the Uicolored Jay (*Aphelocoma unicolor*), but it does breed cooperatively and exhibits behavioral characteristics intermediate between those of Florida Scrub-Jays and Mexican Jays: intermediate group sizes, a single female breeder, and possibly more than one breeding male per group (Pitelka 1951, Webber and Brown 1994).

The occurrence of cooperative breeding in the Florida Scrub-Jay, Mexican and Uicolor jays, in one population of Western Scrub-Jay (*A. californica sumichrasti*), and in some or all species studied in closely related genera (*Cyanolyca*, *Cyanocorax*, *Cissilopha*, and *Calocitta*; reviewed in Brown 1987), suggests that cooperative behavior is a primitive character state shared with other Middle and South American jays (Edwards and Naeem 1993). Indeed, even other more distantly related corvids exhibit varying aspects of group living and cooperative breeding (e.g., Gray Jays, *Perisoreus canadensis* [Waite and Strickland 1997]; western American Crows, *Corvus brachyrhynchos hesperis* [Caffrey 1992]), and a wide variety of other avian taxa show at least facultative or incidental helping behaviors (see Brown 1987). If group living and cooperative breeding are ancestral and Western Scrub-Jays have lost the behavior (Pitelka 1986, Peterson and Burt 1992; but see Brown and Li 1995), why then are California Scrub-Jays so adamantly noncooperative?

OVERVIEW

Proposed hypotheses and models have invoked a variety of ecological, demographic, and behavioral processes as key factors in the evolution and maintenance of group living and cooperative breeding. Most theories for the evolution of group living and cooperative breeding postulate that social groups form because individuals lack opportunities to disperse and breed successfully themselves. Such opportunities may be limited by a shortage of mates (Rowley 1965, Pruett-Jones and Lewis 1990); by the ability of groups, but not pairs, to breed successfully (Rabenold 1984, 1985; Austad and Rabenold 1985, 1987); and by a high variance in resource levels and carrying capacity, leading to either a high cost of independent breeding (Emlen 1982), to closures of intermittently open breeding vacancies (Brown 1987), or a general lack of suitable breeding territories (Selander 1964; Brown 1974, 1978). Other theories stress the importance of the distribution of habitat quality (Koenig and Pitelka 1981) or the variance in territory quality (Stacey and Ligon 1987, 1991) in selecting for delayed dispersal and group living. Others point out that where resource renewal is slow, group size may be limited to pairs, despite other factors favoring retention of offspring (Waser 1981, Brown 1982). Finally, virtually every study of cooperative breeders suggests significant direct or indirect inclusive fitness benefits, or both, accruing to individuals that delay dispersal and assist their parents or siblings in some manner. Although California Scrub-Jays do not delay dispersal and help, ancestral populations almost certainly did so, and the loss of the fitness benefits associated with group living and cooperative breeding must be taken into account.

Examining the importance of these factors requires data on food resources and foraging, territorial behavior and territory quality, dispersal, reproduction, and survivorship. Such information for the California Scrub-Jay is presented in the central sections of this monograph. An essential part of the comparisons among populations must focus on non-

breeders: helpers in cooperative species, floaters in noncooperative ones. Acquiring data on nonbreeding floaters is notoriously difficult, and floaters have most often been ignored or written-off as "surplus population." Floaters are, of course, as integral to a population as nonbreeding helpers, and are a primary focus of this monograph.

The penultimate section of this volume uses these data to draw comparisons among *Aphelocoma* jays and to test the predictions of the various models and hypotheses. It should be noted that these models approach the evolution of group living and cooperative breeding as proceeding from an earlier noncooperative state. Here, the transition is from an ancestral cooperative state to a noncooperative one, and there is no a priori reason to suspect that evolutionary factors are symmetrical in their effects. This may also complicate comparisons among populations in that certain behaviors may be relics of an ancestral cooperative social system.

In the final section, I show how specific factors affect Western Scrub-Jays in California—from the pattern of acorn production to the suite of strategies available to floaters for gaining a territory—and contribute to the loss of cooperative breeding while favoring early dispersal and floating.

STUDY AREA AND METHODS

LOCATION OF STUDY AREA

The 900-ha Hastings Natural History Reservation lies in the outer coast range of central California at the upper end of the Carmel Valley, 36 km from the Pacific Ocean. To the southwest the Santa Lucia Range rises to 1,538 m on Chews Ridge, and to the east Palo Escrito Peak tops the Sierra de Salinas at 1,362 m (Fig. 1).

I studied scrub-jays primarily on Big Creek, in the lower portion of the Reservation.

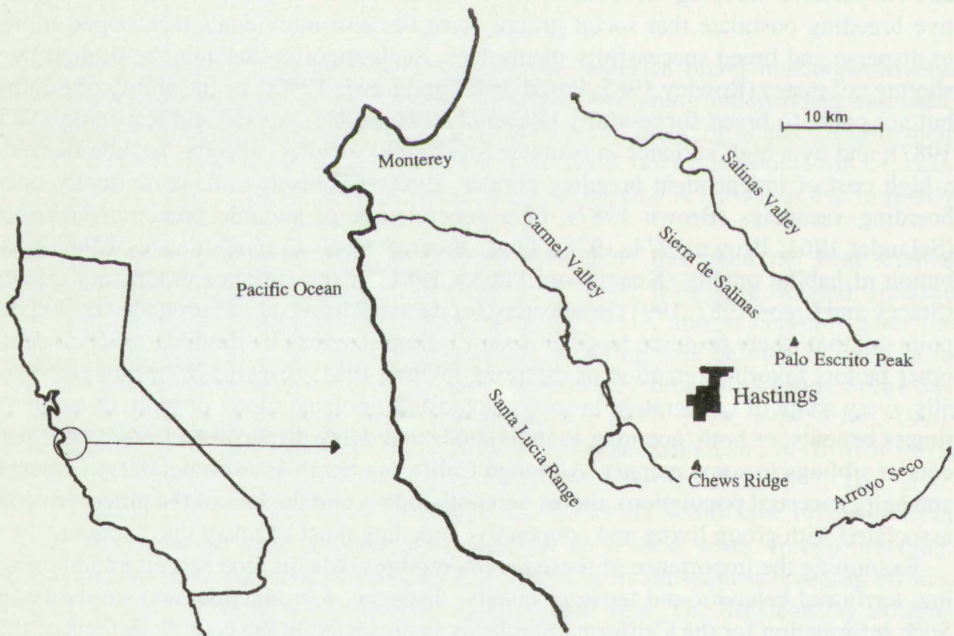


FIGURE 1. Location of the Hastings Reservation in relation to local geographic and topographic landmarks.