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.

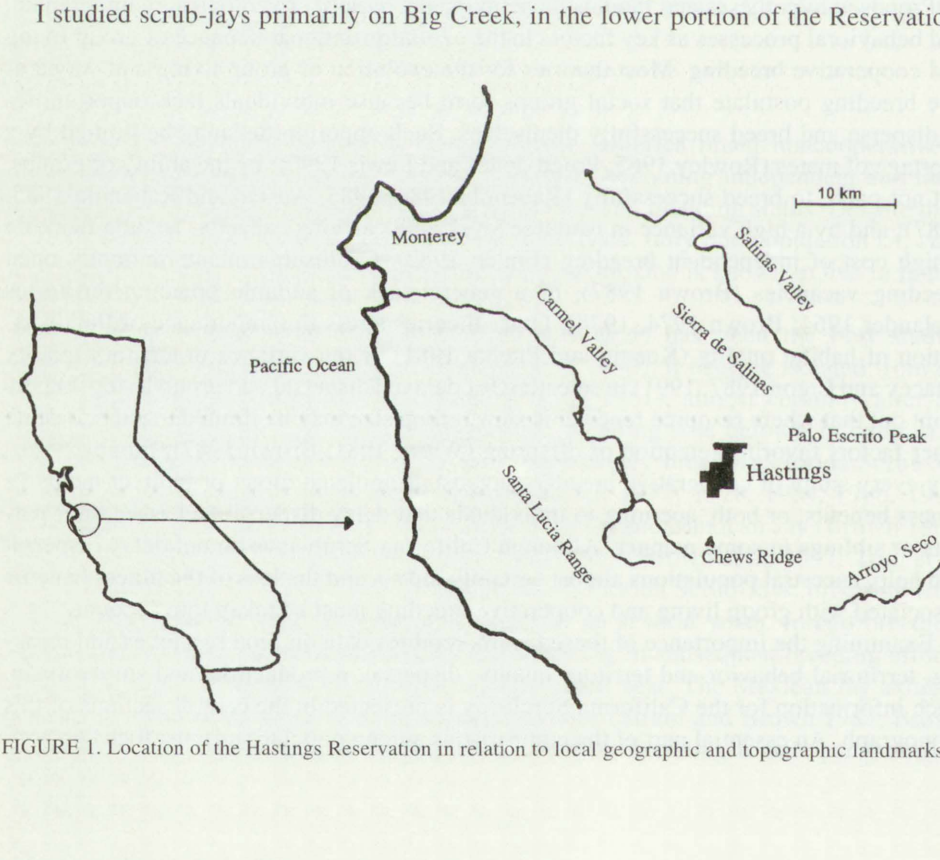

FIGURE 1. Location of the Hastings Reservation in relation to local geographic and topographic landmarks.

Big Creek flows through the center of the site, and four hills (470–637 m) rise nearby (Fig. 2). In 1981, the first year of the study, the study area covered 83 ha, and in 1982 through 1985, 197 ha. Within the study area all major vegetation and habitat types found in the surrounding area are represented. Other parts of the Reservation, and neighboring ranches, were surveyed occasionally for floaters and to monitor dispersal.

CLIMATE

The Reservation has a Mediterranean climate; the summers are dry and warm, and the winters wet and cold. Almost no rain falls between May and October, and late summer and early fall are extremely hot and dry. Rainfall over the last 40 years has averaged 52 cm. Mean monthly temperature and precipitation are roughly inversely related. July is the hottest and driest month; the wettest months are December through March. Figure 3 presents 40-year averages for temperature and precipitation at the Reservation headquarters, at the center of the study area. The creeks stop flowing in late summer in most years; Finch and Robertson creeks always hold some pools through the summer whereas Big Creek dries up completely. Snow falls on the higher elevations of the Reservation several times in most winters, but rarely persists for more than a day.

VEGETATION

Vegetation is predominantly oak woodland and is similar to foothill vegetation found throughout the central coast ranges. Six important plant communities, as defined in

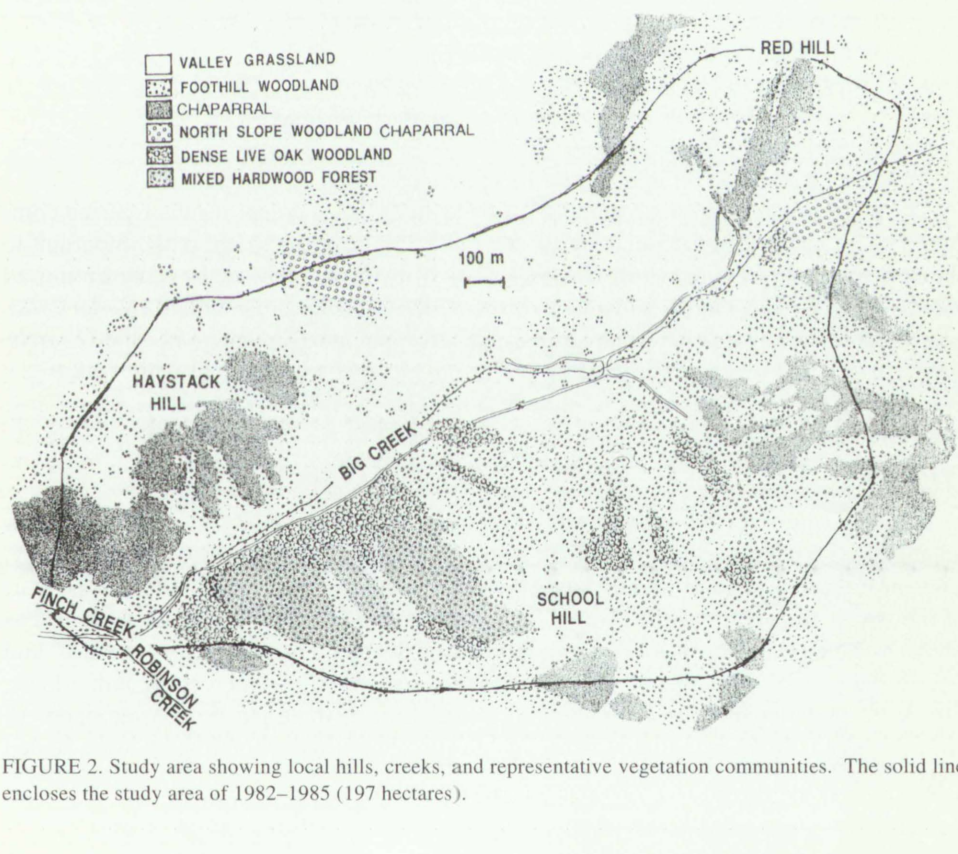

FIGURE 2. Study area showing local hills, creeks, and representative vegetation communities. The solid line encloses the study area of 1982–1985 (197 hectares).

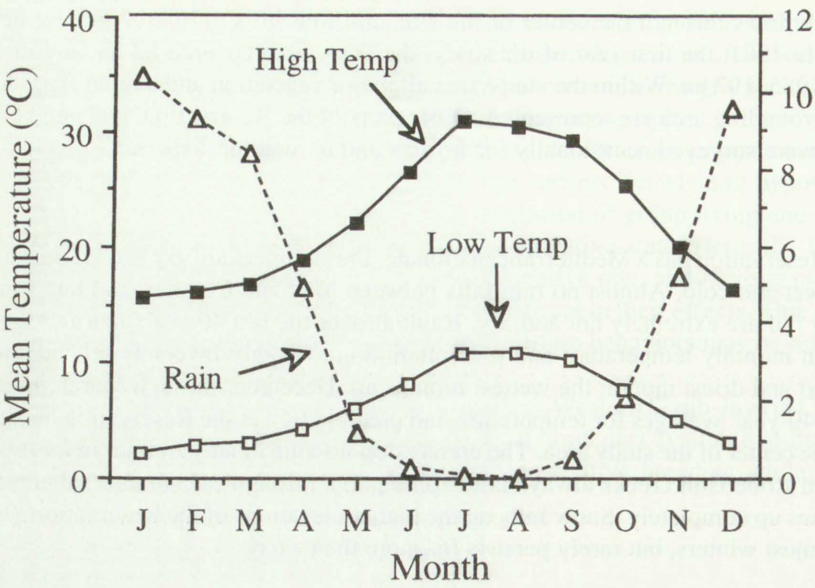

FIGURE 3. Forty-year mean rainfall and mean maximum and minimum temperatures at the Hastings Reservation (1938–1978).

Barbour and Major (1977), are found on the scrub-jay study area:

1) Mixed hardwood forest (*Quercus agrifolia-Arbutus*).
2) Foothill woodland (*Q. lobata-Q. douglasii*).
3) North slope woodland-chaparral (*Aesculus californica-Q. agrifolia* phase).
4) Chaparral (*Adenostoma fasciculatum-Ceanothus cuneatus*).
5) Riparian forest (*Salix-Platanus* phase).
6) Valley grassland (*Bromus-Avena-Erodium*).

The distribution of these communities on the study area (except for the riparian communities) is mapped in Figure 2. By far the most dominant trees, and most important to the scrub-jays, are the oaks. On the Reservation there are six species representing all three oak subgenera. On the study area, three of these species are common (*Q. agrifolia*, *Q. lobata*, and *Q. douglasii*) whereas *Q. kelloggii* is rare and *Q. chrysolepis* and *Q. wizlizenii* are absent; however, *Q. kelloggii* and *Q. chrysolepis* are abundant within 1 km.

METHODS

Banding

Between July 1977 and March 1981, prior to the start of this study, 43 jays were banded, either with color bands or with U.S. Fish and Wildlife Service (USFWS) bands only. Eleven of these jays were found as breeders on the study area in April 1981 at the start of the study. Beginning in 1981, my field assistants and I banded 779 scrub-jays: 106 as breeders, 350 as nestlings, and 323 as nonbreeding floaters. I use the terms "breeder" and "territorial jay" interchangeably; floaters are nonterritorial and nonbreeding individuals. Jays were given unique band combinations consisting of three plastic colored bands (8 colors) and a USFWS aluminum band. The plastic wrap-around color bands were sealed with acetone.

I captured breeders and floaters almost exclusively with ground traps baited with acorns, but a small percentage was captured with mist nets at water sources in July through September. Nestlings were banded at 10 days of age.

Age determination

When first caught, scrub-jays were aged according to molt and feather wear (Pitelka 1945). I use the following terminology to describe age classes:

1) juveniles (up to five months old): individuals between fledging and near conclusion of post-juvenile molt (approximately 1 October). Juveniles have gray heads and other less obvious plumage characteristics that separate them easily from other age classes.

2) first-year birds (up to 12 months old): individuals from fledging through the next spring (31 May). Thus I refer to jays breeding in the spring following hatching as first-year birds. In the post-juvenile molt, jays molt their body feathers, but most flight feathers (and coverts) are retained (Pitelka 1945). This allows first-year jays to be distinguished from adults easily in the hand and, with practice, in the wild.

3) adults (+12 months old): all individuals after the first spring (1 June) following hatching. Between June and September three age classes could be identified: juveniles (young of the year), second-year jays (hatched the previous spring, entering their second year and undergoing their first complete molt), and jays entering their third year or older.

Sex determination

All breeders were sexed by behavioral criteria; only females incubate, brood young, and give the sex-specific "rattle call." Females are also slightly smaller, duller in plumage, and weigh less than their mates. Side by side, the sexes of a known pair are usually easily recognized.

Floaters could not be sexed in the field unless a female gave a rattle call, or a male engaged in courtship feeding with a known female floater. To ascertain the sex of floaters I performed discriminant function analyses, based upon weight and wing-cord measurements on breeders and floaters from the study area, all of known sex. The single discriminant function (N = 150, $\chi^2 = 133.9$, df = 2, $P < 0.001$) correctly classified 89% of 79 females and 89% of 71 males. An independent data set was taken from museum specimens (University of California Museum of Vertebrate Zoology) collected on or near the Hastings Reservation. These 36 females and 25 males included only adults and first-year birds. The discriminant function derived from the first sample correctly classified 93.4% of the independent data set (94.4% of females and 92% of males) and was then used to sex the floaters captured on the study area.

Nest checks

I attempted to find every nest each year as early as possible in the breeding season. Beginning in late February, I began monitoring the banded breeders and tried to locate nests during nest building, when the task is easiest. After egg laying, the jays become secretive and locating nests often took hours or several days. Locating nests was difficult because jays may nest from 0.5 to 15 m above the ground in shrubs, lichens, mistletoe, old magpie nests, and in oak canopies. My attempts to entice nest-building females with nesting material in order to follow them back to the nest, as is sometimes possible with Florida Scrub-Jays (G. Woolfenden, pers. comm.), proved unsuccessful.

Nearly all nests were found before or soon after egg laying. A few nests were lost to predators before they were located, but even in those cases I knew, from the pair's behavior, whether the pair had a nest with eggs. For example, prior to egg-laying the pair would be vocal and easily observed; after egg-laying the female would rarely be seen, and the male would be comparatively unobtrusive and would collect food to feed to the female. I failed to locate only one nest that successfully fledged young (out of 215 pair-years and a total of 315 nests).

Once located, nest checks were kept at a minimum. I visited only to determine first egg date (FED), clutch size, and hatching brood size, and to band the nestlings. The jays vociferously defend their nests and thus may attract any of a suite of predators. My activities, primarily in 1981, led to the loss of nests by attracting other scrub-jays, American Crows, Yellow-billed Magpies (*Pica nuttalli*), and Cooper's Hawks (*Accipter cooperii*). To minimize the impacts of my activities, nests were checked with a mirror attached to a 1-m staff, and in many cases I did not need to approach the nest closely until banding. Nests that were difficult to reach were checked only at the estimated hatching date and at banding, or just at banding to minimize the chance of attracting predators. This resulted in some loss of data, but minimized bias due to human interference; in cases where I thought my activities caused nest or nestling loss, I excluded the record from all analyses.

Nests were visited on the estimated day of fledging to count the number fledging, and then one month and two months later to count the number of independent young. Although young may be fed up to three months after fledging, they usually disperse from their natal territories 7 to 8 weeks after fledging. Between nest checks, pairs and nests were watched to confirm whether the nests were still active. If not, the nest was examined to determine cause of loss, and the new nest (if any) subsequently located. Local scrub-jays fledge only one brood per year but will renest up to three times if earlier nests fail.

Territory mapping

Beginning in March of each year, locations of the banded breeders were recorded on aerial photographs (1 cm = 12.5 m) of the study area. In addition, defended boundaries were marked where disputes occurred. By August, the accumulated locations and defended boundary locations were used to delineate territories. Although I mapped territories only during the breeding season, pairs defended their territories throughout the year. Changes in boundaries may occur at any time, usually as a result of breeder death; such changes and their presumed cause were noted. Throughout this volume specific territory names are indicated in capitals, e.g. BURNT, 2400R, NTN, and can be located on the territory maps.

Operationally, I use both defended area (Noble 1939) and exclusive use (Pitelka 1959) to define the territory boundaries. In some cases, especially where territories were not apparently contiguous, I used a tape recorder to play vocalizations to attract breeders and locate borders. Territory size was measured by tracing boundaries with a digital planimeter; no compensation was made for differences in slope.

Vegetation sampling

Two methods were used to sample vegetation characteristics. First, vegetation throughout the Reservation was measured (W. Koenig, unpubl. data) employing the methods of James and Shugart (1970). On 0.04 ha plots (N = 246) placed every 60 m on a grid, the following were recorded: (1) the species and diameter at breast height (DBH) of all trees; (2) estimates of percent coverage of tree canopy, shrubs, and grass; and (3) the species of trees observed within the 60 m grid unit but not within the 0.04 ha plot. Each sample covered approximately 10% of the total area of a grid unit.

Second, on aerial photographs of the study area, I used a digital planimeter to measure the following on 24 territories: (1) total area; (2) area of canopy cover of oaks; (3) area of canopy of other trees; (4) area of chaparral; (5) area of other brush; and (6) area of open grassland. These data were used to relate vegetation characteristics to occupied and unoccupied habitats and to the overall quality of territories.

Breeder censuses

The study population of banded breeders was censused periodically to acquire data on survivorship and breeder movements. Censuses occurred in early October, early January, early April, and early July, and pairs were monitored on a weekly basis from mid-March to mid-July in conjunction with nest checks. Each complete census took 10–14 days.

Floater censuses

During 1981–1982 and 1982–1983, monthly surveys were conducted on all territories and unoccupied areas on the study area. In each location the number of floaters (nonterritorial jays) was estimated. Floaters, especially during the nonbreeding season, tended to aggregate and to be vocal, bold, and easily observed. Many were banded, and I remained on an area until most sightings were repeats. In areas with no apparent floaters, I remained at least 1 h, during which I played vocalizations from a tape recorder to attract any jays in the area.

Floater sightings

In the course of the study, floaters were identified by their color bands, and their location was noted. Over 2,196 resightings of 276 color-banded floaters (including jays born on the study area and immigrants) were recorded. These data were used to examine juvenile dispersal, floater associations, floater movements, and the transition from floater to breeder status.

Behavioral observations

Between August 1981 and March 1984, I collected time-activity budgets on territorial breeders. Focal-animal sampling (Altmann 1974) on each individual lasted for 1 to 4 h (mean of 3 h). A composite day for each individual was completed over a one- or two-day period. I made a continuous record of all behaviors, with transitions between behaviors recorded to the nearest 10 s. Each hour was considered an individual sample period, and percentage of time in different activities was calculated as a percentage of time the jay was in view. Particular attention was focused on foraging behavior and method (e.g., leaf gleaning, hawking, caching acorns, recovering acorns), and territorial behavior (e.g., breeder-breeder and breeder-floater interactions). Data were collected every month (mean of 35 h per month) between July 1981 and March 1984, except for January through March and October through November 1983. Because I was able to follow individual floaters for only short periods, I quantified foraging behavior by recording the second foraging movement after initial contact on each individual. This was also done for breeders so that breeder and floater foraging behavior could be compared directly.

Radio-tracking

Floaters were radio-tracked to acquire data on juvenile dispersal, home-range movements, and habitat use. Radio backpacks were glued to the backs of jays and further secured with a harness (5 g total weight). Radio batteries lasted from 4 to 10 weeks. Radios were placed on 16 birds: (1) three juveniles five weeks post-fledging, just prior to dispersal in 1984; (2) two first-year floaters during the winter, 1984–1985; and (3) 11 floaters during the breeding season in 1985 (one adult, 10 first-year jays). Jays were followed for 3-h periods, and locations marked on aerial photographs every 10 min. From observations over one- or two-day periods, composite days were compiled from morning, midday, and evening watches. During the watches, in addition to locations, data were collected on interactions with breeders, other floaters, and foraging behavior. The tagged jays became accustomed to observers and could usually be kept in sight. In all, 618 h of radio-tracking data were collected on tagged jays. I also performed 27 "simultaneous" locations on all of the tagged jays during the breeding season in 1985 to detect grouping.

Food assessment

Scrub-jays eat a wide variety of foods, which makes sampling resources difficult. I settled on several methods to estimate the relative abundance of two important foods: insects during the breeding season, and acorns in the fall. The relative abundance of flying insects was measured with a series of 9 yellow pan traps filled with water and surface tension broken with a drop of liquid dish soap (Southwood 1978). The yellow pans were emptied weekly, and the collected insects classified to order, dried, and weighed (W. Koenig, unpubl. data). Data on relative abundance of ground and grass dwelling insects were provided by P. Williams, who performed weekly sweep-net samples during the breeding season. These samples consisted of 100 sweeps of a butterfly net across an open field (valley grassland community) at the center of the study area. Collected insects were dried and weighed. I attempted to estimate the relative abundance of lepidopteran larvae, the major food of young nestlings (Verbeek 1970; pers. obs.) by examining 1,000 oak leaves weekly (Perrins 1976). Even when the jays were gleaning large numbers of larvae, the only kind I counted in sufficient numbers were those of the California oak moth (*Phryganidia californica*), which is not eaten by jays. The relative abundance of acorns was visually estimated each fall (Carmen et al. 1987, Koenig et al. 1994a). We sampled 250 oaks of five common species. On each tree, two observers counted as many acorns as possible in 15 s and the two counts were combined for "acorns per 30 s." Each tree was also scored on a scale from 0 (no acorns) to 4 (a bumper crop). In addition, four traps were placed under each of two trees of each species to determine the temporal pattern of acorn fall.

FOOD AND FORAGING

Food abundance and foraging behavior have fundamental influences on the social behavior of birds. Verbeek (1970) and Brown (1974) hypothesized that the differences in social behavior in jays and other corvids were primarily the result of the various exploitation patterns resulting from patterns of food abundance and foraging behavior. A distinct and important behavior that all jays share is food caching; numerous species of birds, including *Aphelocoma* jays, cache food (Smith and Reichman 1984, Vander Wall 1990), primarily seeds, and studies have shown that differences in annual seed