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

abundance affect the timing of reproduction, reproductive success, and behavior of seed caching birds (Perrins 1970, Vander Wall and Balda 1977, van Balen 1980, Koenig and Mumme 1987). In this section, I examine how food abundance and foraging behaviors of scrub-jays varied seasonally and annually, and how this variation affected their social behavior.

Seasonal Abundance of Food

Many studies at Hastings have measured food resources thought to be important to several avian species. These data give a broad picture of average seasonal variation in scrub-jays' food availability. Early in the breeding season, jays forage predominantly by leaf-gleaning when oak-leaf arthropods are available, especially on live oaks (*Q. agrifolia*; Fig. 4a). Grasshoppers are important later in spring and early summer, and their abundance shows an abrupt rise in May and decline in July in most years (Fig. 4b). During this study, other research workers and I quantified the relative abundance of ground-dwelling invertebrates (P. Williams, unpubl. data; Fig. 4c) and flying insects (W. Koenig, unpubl. data; Fig. 4d). These data indicate that invertebrate abundance is typically low in March through mid-April, increases sharply in late April, and peaks in May and early June. By August, with the onset of the late summer dry period, all samples of invertebrate abundance decrease.

Although seasonal buildup and total relative abundance of invertebrates differed among years, variation in acorn abundance was even greater. In a 12-year study of acorn production patterns at the Hastings Reservation, the oak species tended to produce acorns asynchronously, with crop failures occurring every 4 to 7 years; the probability of an poor acorn crop was directly related to the number of oak species in the area (Carmen et al. 1987, Koenig et al. 1994b). Between 1971 and 1987 three crops failed; two (1973 and 1983) were localized and affected lower elevations of the Reservation (MacRoberts and MacRoberts 1976, Carmen et al. 1987), one in 1978 was extensive (Koenig and Mumme 1987). Over the study period, acorn production was good in four years and poor in one (1983, Fig. 5). In the poor year, however, acorns were abundant within 3 km of the study area.

Another important factor in acorn availability is the length of time acorns are retained on the trees, being greatest in *Q. agrifolia* (Fig. 6). Once acorns fall they are rapidly lost to acorn consumers; in contrast, those on the tree are available to just a few seed eaters, and therefore represent a valuable and long lasting food resource for jays, both for immediate consumption and for caching.

Seasonal Foraging Behavior of Breeders and Floaters

Foraging of breeders

A total of 2,456 foraging observations on territorial jays (minimum of 100 observations in any month) were recorded between July 1981 and December 1982, years with good acorn crops. Foraging activity was expressed as a proportion of all observations, with observations from the same month in different years pooled (Fig. 7). Beginning in August and continuing through February, acorns eaten directly off the tree or from the ground ranged from 16% of all recorded foraging events in February to 31% in October. Jays began storing acorns and, to a lesser degree insects, worms, and other foods, in large numbers in September (25% of all foraging activity), and continued to do so into March

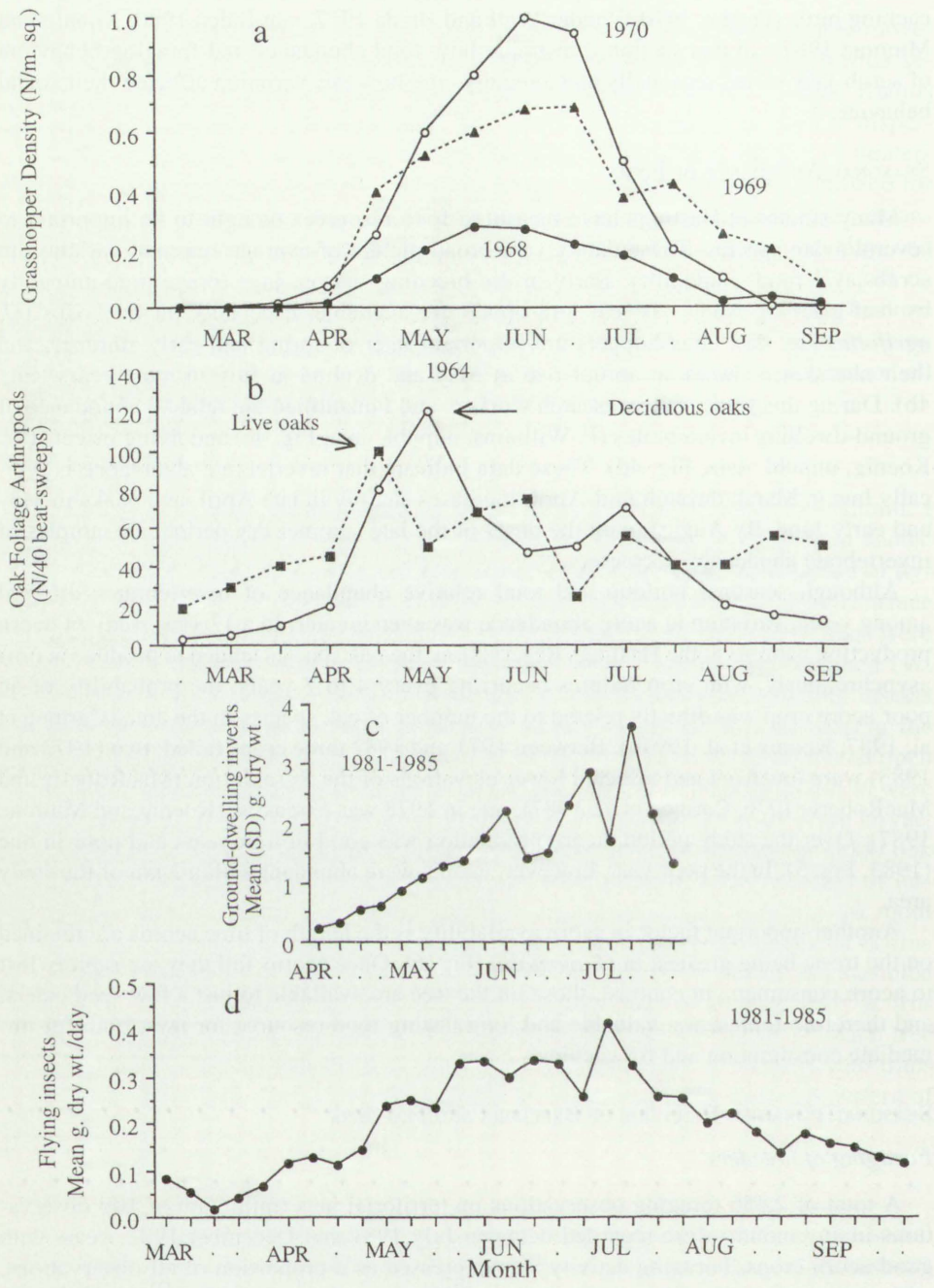

FIGURE 4. Relative abundance and seasonality of invertebrates at the Hastings Reservation: a) grasshopper density 1968–1970 (Verbeek 1970); b) oak-foliage arthropods from beat-sweep samples in 1964 (Root 1967); c) ground-dwelling invertebrates from sweep-net samples 1981–1985 (P. Williams, unpubl. data); and d) flying invertebrates from yellow-pan catch traps, 1981–1985 (W. Koenig, unpubl. data).

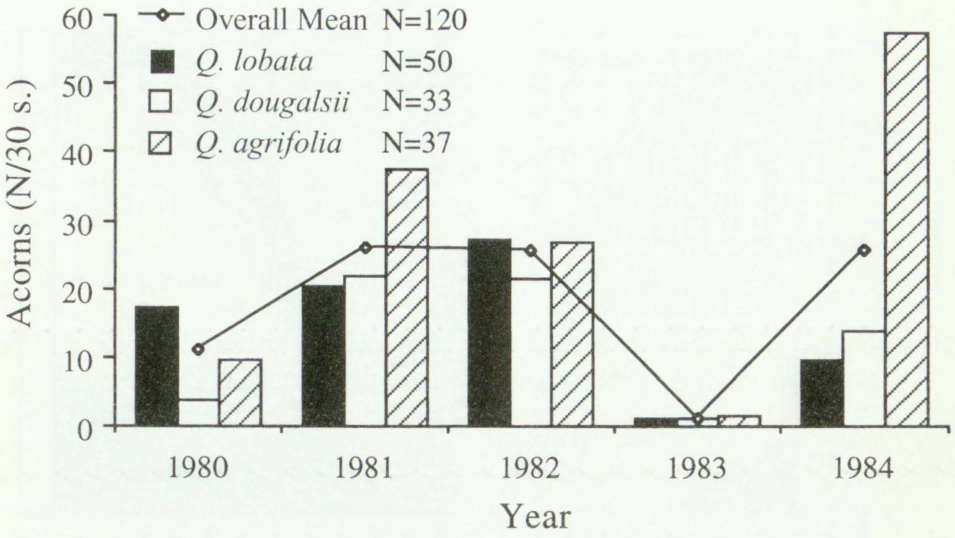

FIGURE 5. Relative abundance (30-s counts) of acorns produced by the three common species of oaks on the scrub-jay study area from 1980–1984. The line indicates overall mean for the three oak species.

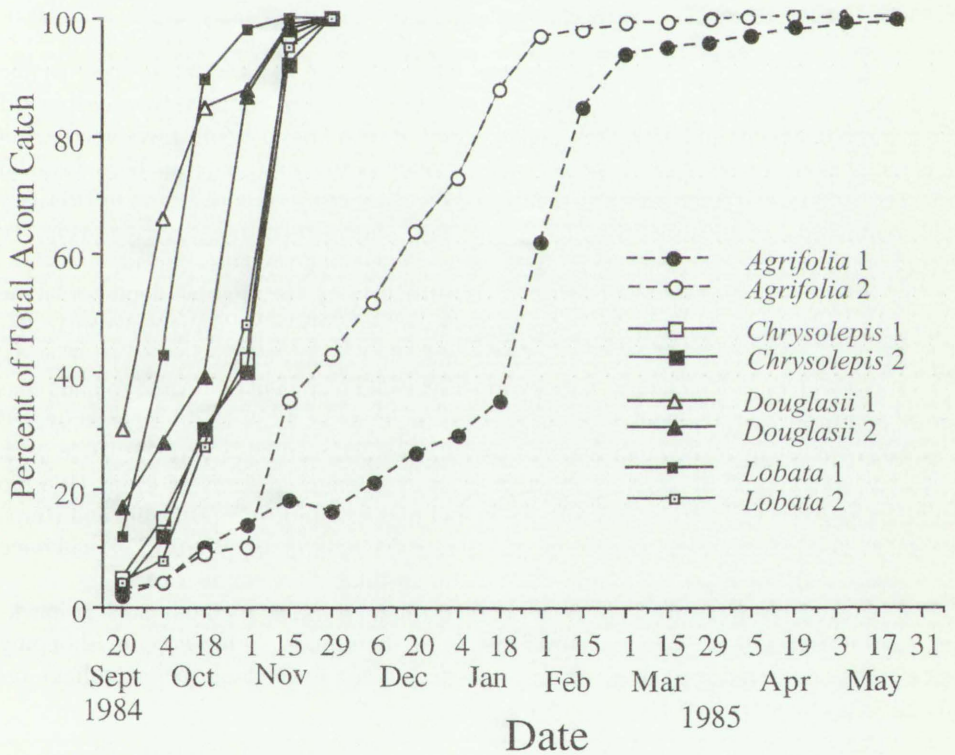

FIGURE 6. Seasonal pattern of acorn fall for two individuals each of four oak species shown as the cumulative percentage of total fall. Data are from acorns collected in acorn traps on a weekly basis, with four traps under two trees of each species.

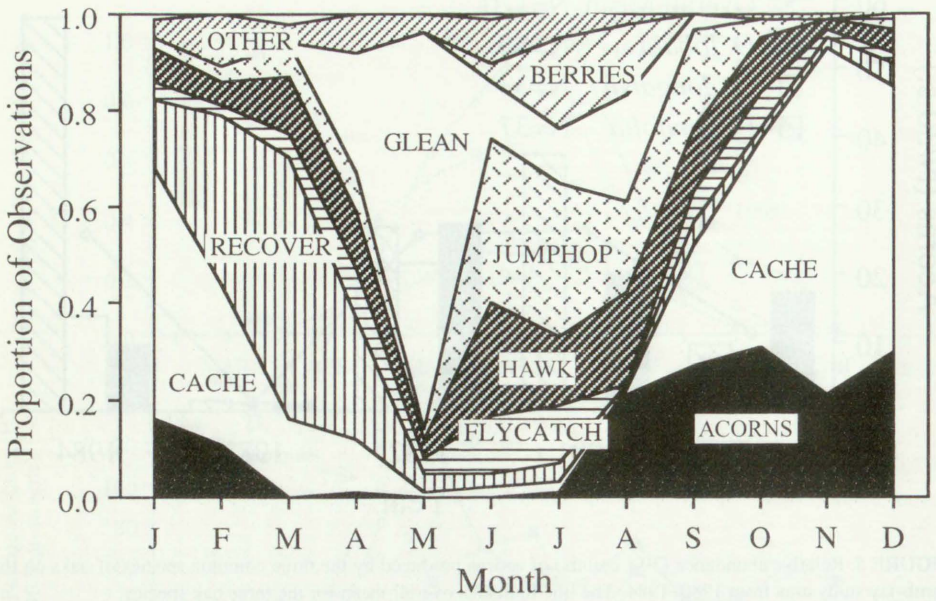

FIGURE 7. Seasonal change in foraging activities of territorial jays over the year expressed as a proportion of all foraging activity (see text for explanation).

(16%). Jays scatterhoarded intact acorns in the ground on their territories; perishable foods (e.g., partially eaten acorns, insects, earthworms, parts of animals) were cached off the ground in lichens and bark. The vast majority of food stored (>90%) was acorns, but jays might store any temporarily abundant food, such as swarming ants and bees. Jays did not recover much stored food until January (14% of foraging activities), but in February and March recovering stored food comprised the better part of foraging effort (Fig. 7). Acorns made up the vast majority of food items recovered during this period.

In April, jays shifted to invertebrate foods, primarily by gleaning lepidopteran larvae from oak leaves; by mid-April and May this constituted 79% of all foraging events, suggesting that such larvae are abundant earlier than other invertebrate foods (see Fig. 4). Lepidopteran larvae, which have a relatively high protein content compared to plant material, constitute approximately 60% of the nestling diet (Verbeek 1970). Jays recovered cached acorns even in May and fed acorns to their older nestlings (Verbeek 1970; pers. obs.). Acorns contain mostly carbohydrates and moderate amounts of lipids (Wainio and Forbes 1941, Ofcarcik and Burns 1971), but high tannin levels (Ofcarcik and Burns 1971), and their detrimental effects on growth rate (Marquardt and Ward 1979) and bone development (Elkin et al. 1978) may make them unsuitable for younger nestlings.

By June and through July, jays used several different foraging methods, such as hawking (flying from low perches to capture insects on the ground), jump-hopping (hopping through the grass and leaf-litter, scaring up insects), and flycatching (aerial sallies), reflecting the wider array of foods available to them.

Acorn use, foraging behavior, and time budgets

I studied time-budgets of territorial jays from August 1981 through February 1984. This period included two years of good acorn production (1981 and 1982) and one (1983)

of local failure. Time budgets from April through July were similar in all years, and breeders spent an average of 71% of all daylight hours foraging (Fig. 8). This sample excludes incubating and brooding females as well as breeders without eggs or nestlings. The high percentage of foraging time, therefore, reflects the high demands of the male foraging for himself and his incubating mate, and both adults foraging for young. In good years, jays reduced their foraging time beginning in August, when acorns became available and began to make up a large part of the diet, and from August through March spent only 36% of the day foraging. In contrast, during the poor acorn year, jays foraged significantly longer, averaging 64% of daylight hours in August and December through February (Fig. 8).

In good years, jays spent an average of 70% of their foraging time (or 25% of total time) from October through March looking for, eating, and caching acorns, compared to less than 10% in 1983–1984 (Fig. 9). Estimated from the time-budget data, each territorial jay cached 5,000 to 7,000 acorns in a good acorn year and spent 16% of foraging time in January, 30.4% in February, and 43% in March recovering and eating them (Fig. 10). In the poor year jays spent less than 1.2% of their foraging time in January and February recovering acorns, and turned to less profitable foods, such as *Avena* grass seeds, and other foraging methods, such as searching through leaf litter, which has been shown to be energetically costly in Black-billed Magpies (*Pica hudsonia*; Mugaas and King 1981). Cached food may be crucial as the breeding season approaches. In good years, scrub-jays laid as early as 15 March, well before most invertebrates were abundant (see Fig. 4). Stored food may be specially important for incubating females that spent long periods on the nest. In another corvid, the Northwestern Crow (*Corvus caurinus*), James and Verbeek (1984) found that without cached food incubating females were unable to maintain normal incubation periods and spent long periods foraging.

Effect of acorn supplementation

Beginning in December 1983 and continuing through March following the acorn crop failure, I experimentally fed four pairs of jays 200 acorns per week. The acorns were placed on feeding platforms at the center of each territory, and the jays removed and stored them within 30 min. The time budgets of these jays closely matched those of jays during the good acorn years and were significantly different compared to unfed jays. For example, foraging time in January was 37% of total time for jays in the good years, and in the poor year 39% for experimentals and 62% for unfed jays; jays spent significantly more time foraging during the poor year (Kruskal-Wallis ANOVA, $df = 2$, $\chi^2 = 10.2$, $P < 0.01$). The difference was due to the lack of readily available stored food; jays in good years spent 15.7% of their foraging time in January recovering stored acorns compared to 15.3% for experimentally fed jays and 1.2% for unfed jays in the poor year. These differences are probably even more pronounced in March, when in good years jays spent only 25% of their total time foraging and 43% of that foraging time recovering stored acorns. Unfortunately, I did not collect time budget data in March of the poor acorn year (1983).

Foraging of floaters

The foraging behavior of floaters was sampled from June 1981 through December 1982 (total N = 2987, minimum of 129 per month). This sample includes only juveniles in June and juveniles and older floaters in other months. No data were collected in May 1982 because all floaters disappeared.

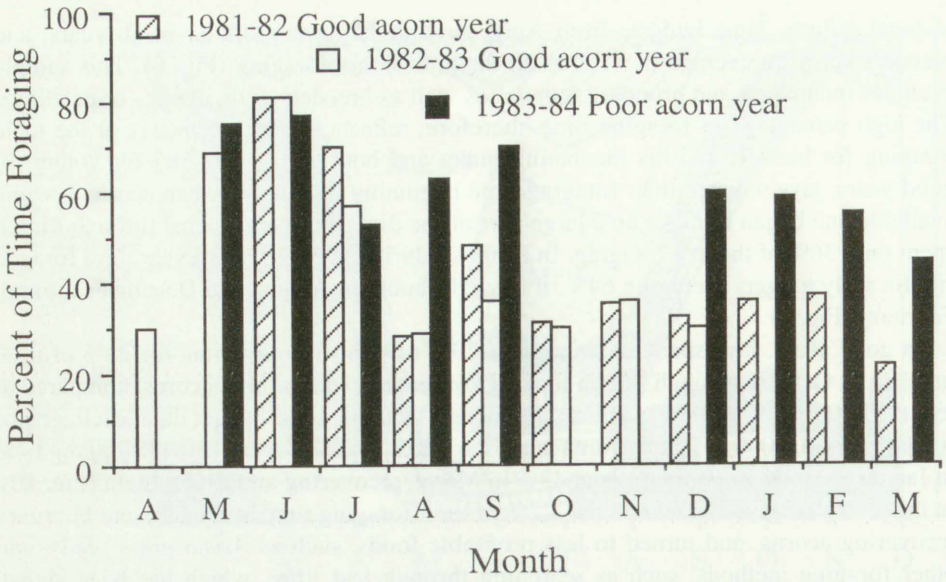

FIGURE 8. Percentage of time territorial scrub-jays spent foraging in two good acorn years and in one poor acorn year. Months without bars indicate no data were taken. Scrub-jays significantly increased their foraging time from August through March in the poor acorn year (Mann-Whitney U, $P < 0.05$ for each paired month). Total sample = 875 h, with a minimum of 18 h per month.

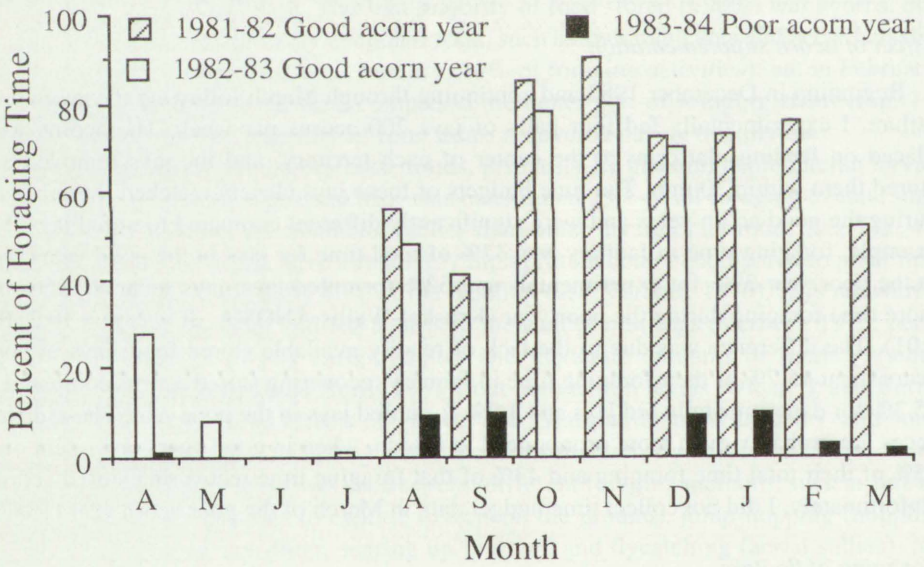

FIGURE 9. Percentage of foraging time territorial scrub-jays spent looking for, eating, caching, and recovering stored acorns in two good acorn years and a poor acorn year. Months without bars indicate no data were taken.

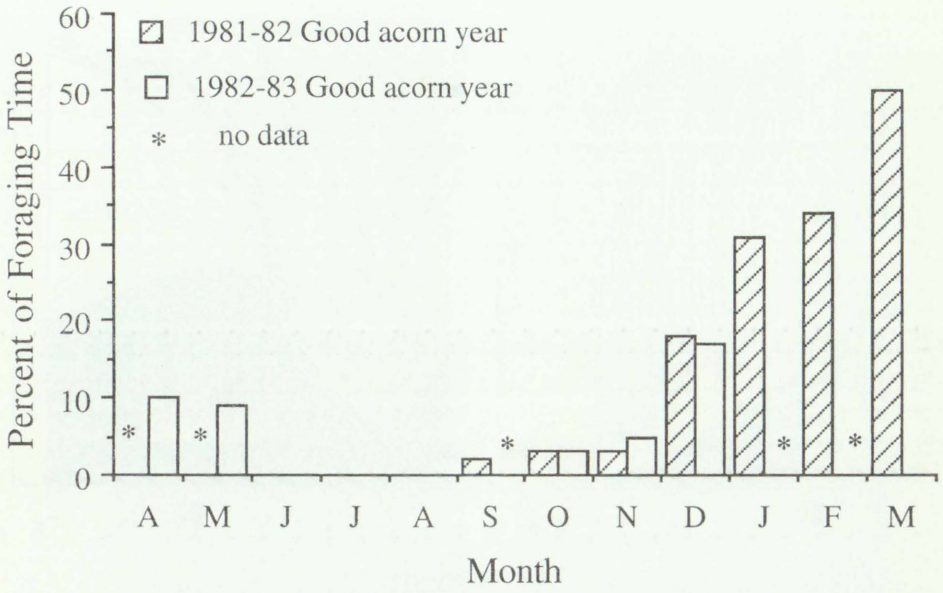

FIGURE 10. Percentage of foraging time territorial scrub-jays spent recovering and eating cached acorns and other cached food during the good acorn years (see text for explanation). Months without bars indicate no data were taken.

The foraging behavior of territorial adults and floaters is similar throughout the year (compare Figs. 7 and 11). The major difference is that young juveniles make heavy use of berries (blue elderberry, *Sambucus caerulea,* and fuschia-flowered gooseberry, *Ribes speciosum*), to which they directed 19% and 52% of total foraging activity in June and July, respectively. Floaters used acorns, stored food, and recovered food in nearly the same proportion as territorial jays and thus seem to be equally dependent on acorns. In 1982 and 1983, floaters disappeared from the study area beginning in April at about the time that territorial jays shifted from stored acorns to lepidopteran larvae. In 1985, when floaters did remain on the study area during the breeding season, foraging behavior of breeders and floaters was identical.

TERRITORIES AND TERRITORIAL BEHAVIOR

Aphelocoma jays are permanently territorial, and those unable to secure a territory are unable to breed. In cooperative species, nonbreeders delay dispersal, live in family groups on their natal territories, and help. In noncooperative populations, nonbreeders float. Differences in territorial behavior, habitat and habitat tolerance, variation in territory quality, and the degree of habitat saturation determine, in large part, the dispersal options available to newly independent young and older nonbreeders, and therefore play crucial roles in selecting for delayed or early dispersal.

Territorial Behavior

Scrub-jay breeders at Hastings rarely left their territories. In several thousand hours of field work I resighted 276 color-banded floaters 2,196 times, but I recorded breeders off their territories only 59 times. Of these, 33 (56%) occurred during the year of an acorn