in the poorest acorn years demand may exceed production for some large groups, but during their 25 years of study, no complete acorn crop failure occurred on the study tract (G. Woolfenden and J. Fitzpatrick, pers. comm.). Whether acorn production declines with time since last burning in Florida scrub oak species as in some other scrub-oaks (Wolgast and Stout 1977) is not known, but this would contribute to low suitability of long unburned areas in Florida for both floaters and breeders. Relatively uniform production of acorns contributes to a situation where nonbreeders would gain little by intruding on neighboring territories, intruder pressure is slight, and territory defense is economical (DeGange et al. 1989). The rarity of acorn crop failures in Florida would also prevent the local populations crashes that occur in California, thereby eliminating the benefits of the wide-ranging movements by floaters (i.e., locating areas where acorn crop crashes have created low population densities and territory vacancies) observed in Western Scrub-Jays.

Mexican Jays and Western Scrub-Jays co-occur throughout much of their range, and although Mexican Jays locally exclude scrub-jays from their preferred habitat, both can be found in oak woodlands that are generally more typical of those in California than those in Florida, that is, with highly variable acorn production (Bock and Bock 1974, Stacey and Bock 1978). However, specific details on acorn production patterns and acorn use and dependency by jays in Arizona are not known.

On the scrub-jay study area at Hastings, the three common species of oaks are distributed as isolated individuals, extensive monotypic stands, and mixed closed-canopy forest. The oaks are generally quite large and a single tree can produce well over 400,000 acorns (W. Carmen, unpubl. data). An average scrub-jay territory at Hastings includes 0.55 ha of oak canopy and two oak species, and although acorn production per territory was not measured, acorns are probably produced far in excess of jay demand in all but the poorest years. Acorn production was highly variable among years, with relatively frequent crop failures on a local habitat level and more rarely on a regional level. Acorn crop failures resulted in territory abandonment, high mortality, emigration by breeders and floaters, and poor reproductive success the following breeding season. Early dispersal and floating allows nonbreeders to respond most efficiently to spatial and temporal variation in acorn production patterns and to locate breeding vacancies. These tactics yield three patterns: (1) localized home-range movements by floaters during the fall-early spring period in most years; (2) emigration to locate acorns during local acorn crop crashes; and (3) either local or wide-ranging movements in early spring to locate breeding vacancies, particularly to areas where population density has been reduced by acorn crop failures.

SYNOPSIS

The fundamental result of this study is that floating should be considered an important strategy for acquiring breeding space, just as is delayed dispersal and helping. When floating is ignored or treated as a one-dimensional phenomenon, not only do theories for the evolution of delayed dispersal and cooperative breeding fall short, but a interesting and complex part of the social behavior of a species is overlooked. Factors that lead to delayed dispersal in cooperative species are known to be complex and may differ substantially among species and populations, and even among individuals within populations and groups. Conditions leading to early dispersal and floating may be equally complex, as are the varied responses of floaters to these conditions. Clearly, opportunities for in-dependent breeding are constrained in both cooperative and noncooperative populations. What then makes early dispersal and floating the preferred strategy in Western Scrub-Jays? Several factors play a part including: (1) the interplay between the pattern of habitat quality and acorn production, (2) the varied behaviors floaters may employ to exploit these resources and acquire breeding space, (3) the behavioral interactions between territorial jays and floaters, and (4) the ability of floaters to settle on low-quality territories and then as breeders to move and improve the quality of their territories. Below, I provide a synopsis of the range of scrub-jay dispersal, movement and behavioral patterns.

Scrub-Jay Dispersal and Floating in Central Coastal California

Figure 41 illustrates a landscape representing an idealized mosaic of habitat qualities for scrub-jays as are found in central coastal California. Higher quality habitats occur where oak diversity is high, live oaks predominate, and insects and berries are abundant. These features are most commonly found along stream channels in the area.

Figure 41a depicts clusters of territories in high- and low-quality habitat (territories in better habitat are more tightly clustered and smaller) and the dispersal movements of floaters during the nonbreeding season (August–April). Tolerance by breeders allows floaters to aggregate in high-quality habitat where acorns are abundant and floater survivorship is expected to be high. As shown, floaters fledged in low-quality habitat move into high-quality habitat, whereas those fledged in high-quality habitat may remain on or near their natal territories; both may also move considerable distances. Floaters appear to be as dependent on cached acorns as breeders and may be closely tied to their stores during the winter. When acorns are few, jays experience significantly higher mortality, reproductive failure, and territory abandonment. Poor acorn production in local areas (e.g., X and Y in Fig. 41a) results in emigration by both offspring and a substantial number of territorial breeders. They search for locations with high acorn production in which to spend the fall-early spring period.

Beginning in April, floaters and residents are less dependent on their cached acorns as invertebrate food becomes more abundant. This seasonal pattern of food abundance may contribute to the tolerance of floaters by local, settled breeders in the winter (when acorns are superabundant), and their intolerance in the breeding season (when insect prey is important and starvation rates of nestlings are high). At this time (Fig. 41b), floaters may move out of high-quality habitat where breeding vacancies are few to potentially high-quality habitat where an interval of poor acorn production has reduced breeder density (e.g., area X), or to poor quality habitat where breeding space may be available intermittently for a number of reasons, including frequent poor acorn crops and movement of breeders from there to higher quality habitat. Surviving breeders may also return to the locations they abandoned due to poor acorn production the previous fall, only some of which are able to reestablish their territories. In such areas in high-quality habitat, occupied space is unchanged but territory size has increased (Fig. 41b area X); in low-quality habitat, territories simply may be abandoned and the space go unused (area Y). Over time breeding density returns to prior levels as new territories are established.

At the onset of the breeding season, individual floaters employ different behaviors, including establishing pseudo-territories, sneaking through territories and unoccupied habitat and, as observed in one year, moving substantial distances in large cohesive flocks (as indicated by the large arrows in Fig. 41b). Floaters also may remain in aggregations

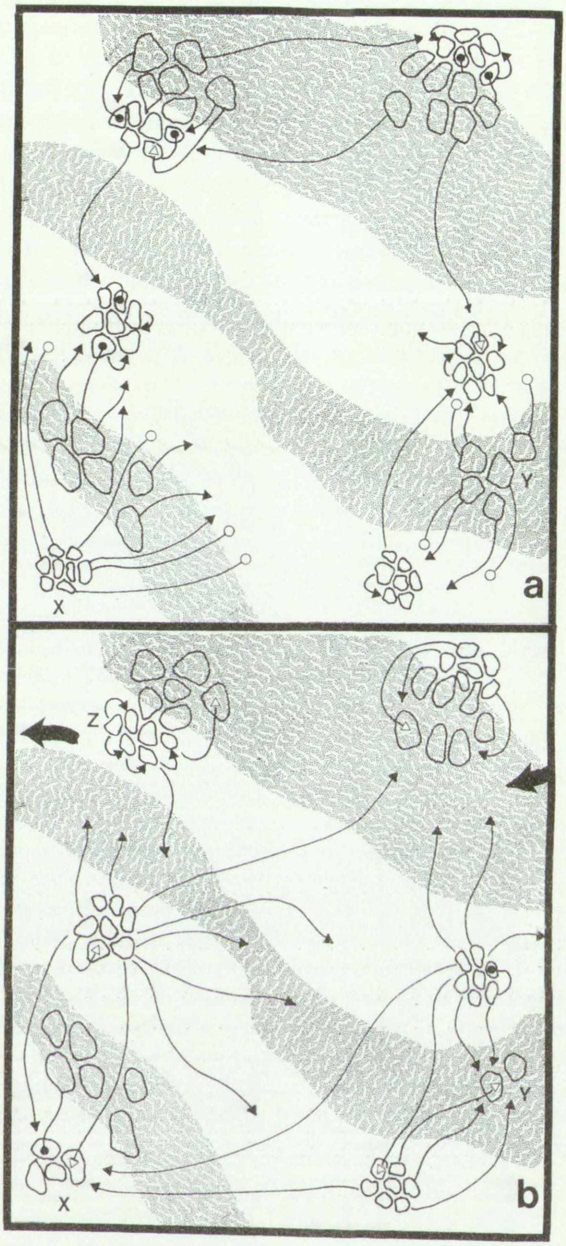

FIGURE 41. Floater and breeder (territorial jay) movements in an idealized mosaic of habitat qualities as found in central coastal California. The unshaded area represents high-quality habitat and the shaded area low-quality habitat. A few representative territories are drawn showing smaller, denser territories in high-quality habitat. Lines with closed arrows denote movement of floaters, open arrows denote floater-to-breeder transition, closed circles denote breeders changing territories, open circles denote breeders abandoning territories, and large arrows denote flock movements. Poor acorn crops occur in area X and Y with exceptional production in area Z. (a) Movement patterns during the nonbreeding season (August–April). (b) Movement patterns during the breeding season (May–July).

on high-quality habitats throughout the breeding season (e.g., area Z in Fig. 41b) as a result of increased tolerance by breeders given unusually abundant acorns into the summer months.

During the year, floaters search for and fill available breeding vacancies as shown in Figure 41. Although breeding vacancies arise from breeder death throughout suitable habitat, floaters have the greatest probability of gaining a breeding vacancy either in poor quality habitat where breeder turnover may be greater or in high-quality habitat where breeder density has been reduced by an acorn crop failure. Also as shown in Figure 41, there is movement of breeders from one territory to another, often from lower to higher quality habitat. Not illustrated are the relatively rare regional acorn crop failures that may result in breeder density decline and subsequent low reproductive output over a broad area, providing increased opportunity for dispersing offspring and older floaters to gain a territory and breeding status.

These patterns of habitat quality and acorn production, the varied behaviors floaters employ to acquire breeding space and exploit resources, the behavioral interactions between territorial jays and floaters, and the ability of breeders to move and improve the quality of their territories all promote selection for early dispersal and floating in scrub-jays in central coastal California, and selection against cooperative breeding.

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