quality territory vacancy, and (3) increasing the survivorship of related breeders (see also Brown 1974, Koenig and Mumme 1987; Stacey and Ligon 1987, 1991). Hence, except for the latter benefit, the general conclusions regarding factors affecting LRS and selecting for alternative dispersal strategies in cooperative and noncooperative scrub-jays are similar. The specific ecological factors that promote delayed dispersal in one population and early dispersal and floating in another are examined below.

TEST OF THEORIES AND COMPARISONS

In this section, I compare data from the California Scrub-Jay with those from several closely related cooperative *Aphelocoma* and other cooperative breeders to test hypotheses and predictions of models for the evolution of cooperative breeding. These comparisons are used to answer the following questions: Do the models adequately explain why one species is cooperative and a closely related species or conspecific is not? What are the critical ecological, demographic, and behavioral differences that select for the alternative social systems in these species? There are, however, three potential complications in drawing conclusions based on such comparisons: (1) the models examined are for the evolution of cooperative breeding, not its loss; (2) it is difficult to separate the effects of historical vs. current ecological factors; and (3) observed behaviors may be relics of ancestral, cooperative populations.

The models discussed are for the evolution of delayed dispersal and cooperative breeding. But are the conditions hypothesized to select for the evolution of a character state such as cooperative breeding the mirror image of those leading to its loss? Not always. In *Aphelocoma* jays, phylogenetic studies reveal that cooperative breeding occurred before the diversification of the genus (Peterson and Burt 1992) and that it was lost in the western North American lineage (Pitelka 1986). Studies of *Aphelocoma* examine factors important to the maintenance of cooperative (or noncooperative) breeding rather than its evolutionary origins; current conditions may not reflect those that led to the evolution of the observed traits and would therefore not be responsible for observed differences in social behavior. For example, cooperative breeding in Australian babblers (*Pomatostomus* spp.) apparently arose in rain forest habitats (Schodde 1982) but has been maintained as the group diversified and spread into arid interior Australia; cooperative breeding still occurs but under far different ecological conditions under which it evolved. In a similar vein, noncooperative populations derived from cooperatively breeding ancestors may exhibit behaviors or demographic components that are relic of ancestral, cooperative populations. In Western Scrub-Jays these may include tolerance of young and nonbreeders on territories, delayed breeding, very low reproductive success in territorial first-year birds, and aspects of territorial acquisition.

Despite these potential complications, for the first time detailed ecological, demographic, and behavioral comparisons can be made among closely related cooperative and noncooperative species and may provide evidence of the key factors selecting for a switch from delayed dispersal and cooperative breeding to early dispersal and floating.

BROWN'S THEORY OF HABITAT SATURATION AND GROUP LIVING

Brown (1969) developed a model for the role of territorial exclusion in creating a nonbreeding surplus, and later for group living and cooperative breeding in New World jays and the genus *Aphelocoma* in particular (Brown 1974, 1978; see also Verbeek 1973). This habitat saturation (HS) theory incorporates both ecological and demographic arguments, and with various modifications and elaborations has served as the underlying framework for most other theories for the evolution of cooperative breeding in permanently territorial species.

Brown argues that in nonmigratory, long-lived species residing near carrying capacity in habitats characterized by stable mature vegetation, territory vacancies will be rare, as all suitable habitats will be "saturated." Under these conditions, the best strategy for young birds is to delay breeding and remain on their natal territory. Early dispersal and floating are not precluded, but young that delay dispersal stand a better chance of eventually getting a territory and reproducing successfully due to competitive advantages that come with increased age and experience and through territorial inheritance. And once young delay dispersal, those that "help" relatives are at selective advantage (through direct and indirect fitness benefits) over ones that do not. Advantages also accrue to breeders via decreased defense costs and enhanced reproductive success due to helper aid. In addition, larger groups have a competitive advantage over smaller ones in securing and keeping territorial space. Brown (1974) suggests that this process is self-reinforcing, leading to a build up of nonbreeders and eventually to multi-pair territories and is mirrored in the progression from the noncooperative California Scrub-Jay, to a single breeding pair with helpers as in the Florida Scrub-Jay, and finally to the multi-pair territories with helpers as in the Mexican Jay.

Brown (1974:78) listed six attributes of cooperative as compared to noncooperative breeders under the "K-selection phase" of his model: (1) delayed maturity, (2) higher survivorship, (3) lower reproductive rate, (4) reduced dispersal, (5) a higher proportion of nonbreeders, and (6) narrower habitat tolerance. These predictions are tested below with data from the California Scrub-Jay and provide a framework for exploring other hypotheses as well.

Delayed maturity and the "Skill Hypothesis"

Delayed maturation is common among cooperative breeders, but controversy exists over whether this leads to group living and cooperation per se (Skutch 1961, Lack 1966) or is merely a correlate of some other causal factor(s) (Brown 1978, Lawton and Lawton 1986). Retention of juvenile or subadult morphological characteristics for a year or two could be a consequence of delayed breeding, but such characteristics occur in both cooperative and noncooperative species (Pitelka 1945). Delayed maturation or "lack of skill" in foraging efficiency, territorial defense, predator avoidance, and reproductive skills may favor delayed breeding (Stearns and Crandell 1981; Brown 1985, 1987), and some suggest this may lead to group living and cooperative breeding as well (Skutch 1961, Rowley 1965, Lack 1966; Heinsohn et al. 1988, 1990; Heinsohn 1991).

Numerous studies have demonstrated that young of cooperative breeders are less skillful than older individuals, including those on cooperative *Aphelocoma* jays (Stallcup and Woolfenden 1978, Brown 1985, DeGange 1976, McGowan 1987), but this is also true for numerous noncooperative species that delay breeding (Sæther 1990). It is also true that young nonbreeders may learn from experienced group members (e.g., White-winged Choughs, *Corcorax melanorhamphos* [Heinsohn et al. 1988]; Seychelles Warblers, *Acrocephalus sechellensis* [Komdeur 1996]; White-throated Magpie-Jays [Langen 1996a,c; Langen and Vehrencamp 1999]; and Long-tailed Tits, *Aegithalos caudatus* [Hatchwell et al. 1999]).

Delayed maturation and overall lack of skill in young birds in both cooperative and noncooperative breeding systems is indicated by a steep increase in age-specific reproductive success of breeders. In California Scrub-Jays, Florida Scrub-Jays, and Mexican Jays, reproductive success is quite low at age one and increases to peak at age four or five (Fig. 39). More California than Florida scrub-jays acquire territories as yearlings, but few breed and those that do have very low success. Some of the few Florida Scrub-Jays that acquired a territory their first year bred successfully (Woolfenden and Fitzpatrick 1984). In some cooperative breeders, such as the Gray-crowned Babbler (*Pomatostomus temporalis*), the gonads are usually small and presumably nonfunctional their first year, and do not reach full size until the third year (Brown and Brown 1981b). However, this may be more an inability of young individuals to acquire a territory and breeding status as young Gray-crowned Babblers that are able to acquire a territory and breed are nearly as productive as adults (Brown and Brown 1981b).

In both the Florida Scrub-Jay (Woolfenden and Fitzpatrick 1984) and Mexican Jay (Brown 1974), larger groups are more successful than smaller ones in securing and expanding territorial space. Although this makes it difficult to establish and defend a territory independently, group living and cooperative behavior may in some cases allow young individuals to be more successful breeders than otherwise would be possible by providing aid in feeding young, territorial defense, detecting and fighting off predators, and nest building. For example, inexperienced Florida Scrub-Jays breeding as pairs average 1.24 fledglings/pair, mixed pairs 1.34, and experienced pairs 1.8. With helpers, the same pairs raise 2.2, 2.5, and 2.4 fledglings, respectively; inexperienced (young) and experienced (older) pairs with helpers fledge the same number of young (Woolfenden and Fitzpatrick 1984).

These comparisons suggest that young in both cooperative and noncooperative birds may be less efficient at foraging, exhibit delayed maturity, and lack reproductive skills compared to older age classes. Although lack of skill and delayed maturity in Western Scrub-Jays may also be relic of ancestral cooperative populations, no reason exists to expect that differences in delayed maturity or skill have led to group living rather than having arisen as a consequence of it.

Higher survivorship

Higher survivorship of breeders was predicted for cooperative breeders (as this contributes to lower breeder turnover and fewer breeding vacancies; see Arnold and Owens 1998, 1999) but no significant difference exists among the California and Florida scrub-jays and Mexican Jays (Table 27), or *A. californica obscura*, another noncooperative population (83%; M. J. Alpers, pers. comm.). Survivorship was even higher (94%) in the Island Scrub-Jay (Atwood et al. 1990).

Lower Reproductive Rate

Reproductive rate is not related to social behavior in *Aphelocoma* jays (Table 27). Clutch size is slightly smaller in the Florida Scrub-Jay than in either the Mexican Jay or California Scrub-Jay, although populations of the Western Scrub-Jay in drier habitats have significantly smaller clutch sizes overall (Atwood 1978). Fledging success is lower in California compared to simple pairs in Florida (43% vs. 66%), and considerably lower compared to pairs with helpers (80%).

Percentages of egg and nestling survivorship are similar. In California, 60.6% of eggs laid hatched and 48% of hatchlings fledged. In Florida, for pairs without helpers, 60% of

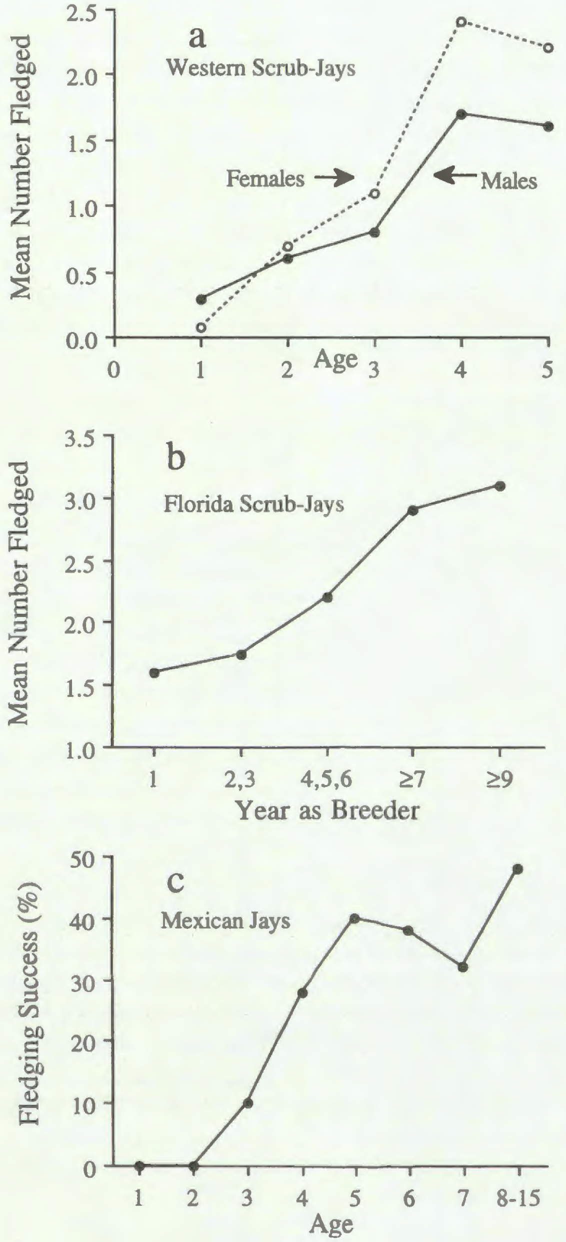

FIGURE 39. Increase in reproductive success with age for the noncooperative California Scrub-Jay, the cooperative Florida Scrub-Jay, and the Mexican Jay. (a) Age-specific reproductive success (fledgling production) in California Scrub-Jay breeders; (b) relationship between past breeding experience and fledgling production in Florida-Scrub Jays (because few first-year jays breed, the *x*-axis begins roughly at age 2; from fig. 8.15 in Woolfenden and Fitzpatrick 1984); and (c) fledging success with age in Mexican Jay breeders (from fig. 3 in Brown 1986).

eggs laid hatched and 54% of hatched eggs fledged. For pairs with helpers in Florida, corresponding values increase significantly to 69% and 68% (Woolfenden and Fitzpatrick 1984). Overall, fledgling production averaged 1.2 per pair at Hastings and 1.59 in Florida, rising to 2.31 for pairs with helpers (Woolfenden and Fitzpatrick 1984).

Given these similarities, what accounts for the higher reproductive output in Florida? First, although nest predation rates are similar, a major difference between the Florida and California populations is the rate of starvation (4.8% vs. 17.2%). Second, virtually all breeding pairs in Florida initiate breeding every year (G. Woolfenden, pers. comm.), and 13% of pairs attempt to raise second broods. At Hastings, however, in 215 breeding pair-years, 40 pairs failed to lay eggs. If these pairs are excluded, the overall average climbs to 1.5 fledglings per pair, quite close to 1.59 per pair without helpers in Florida. Third, pairs with helpers in Florida show a significant increase in fledgling production, which is attributable to lower predation rates on eggs and nestlings compared to those of unassisted pairs.

Reduced dispersal

Comparisons among *Aphelocoma* jays generally support Brown's prediction of reduced dispersal (see also Zack 1990). Mean natal to breeding territory distance in Florida Scrub-Jays is 0.9 territories for males and 3.4 for females (these distances include nearly all dispersal events). In comparison, values from scrub-jays at Hastings were 1.3 and 3.2 territories traversed for males and females; however, these data include but a small percentage of the estimated successful dispersal events. Many California Scrub-Jays float in the vicinity of their natal territories but others make wide-ranging movements and most acquired territories off the study area; hence, actual natal to breeding distances, though unknown, are certainly greater. Brown and Brown (1990) found that Mexican Jays may never leave high-quality territories or at most move to adjacent territories to breed, but their sample was small (6 territories) and evidence of immigration existed.

TABLE 27. Demographic comparisons among *Aphelocoma* jays

	Scrub-Jays			
	California[a]	Island[b]	Florida[c]	Mexican Jay[d]
Breeder survivorship	♂ 0.83	Both 0.94	Both 0.82	0.86
	♀ 0.79			0.81
Mean clutch size	3.7	3.7	3.4	4.0
Mean fledglings/pair	1.2	—	1.4 (pairs)	—
			2.4 (w/helpers)	
Percent non-breeders	♂ 29%	~50%[e]	31%	30%[e]
	♀ 16%		22%	
Age of transition to breeding status (yr)	1–3	2-3	2–3	3–4
Mean age first territorial (yr)	♂ 2.2	—	2.9	—
	♀ 1.6	—	2.4	—
Mean age first breeding (yr)	♂ 2.4	—	3.0	—
	♀ 2.1	—	2.4	—

[a] Estimates derived from demographic values as used in the life tables for females (Table 23) and males (Table 24).

[b] Data from Atwood et al. (1990); clutch size from Atwood (1980b); percent nonbreeders from an independent life table estimate.

[c] Data from Woolfenden and Fitzpatrick (1984).

[d] Data from Brown (1974, 1985, 1986) and Brown and Brown (1990).

[e] Combined estimate, not broken down by sex.

Prebreeders

A salient feature of Brown's (1974, 1978) theory is that permanently territorial noncooperative species either should not have a significant nonbreeding surplus, or that the surplus is due to factors other than habitat saturation, such as an unbalanced sex ratio (Rowley 1965), inability of simple pairs to raise young (Rabenold 1984, 1985), or general lack of skill in young individuals (Brown 1985, 1987).

The "nonbreeding surplus" can be a significant in both cooperative and noncooperative breeders. In field experiments where breeders were removed or high-quality habitat created, breeding positions were filled by nonbreeding helpers in cooperative species (Hannon et al. 1985, Pruett-Jones and Lewis 1990, Komdeur 1991, Walters et al. 1992b) and by floaters in noncooperative species (Watson and Moss 1970, Rutberg and Rohwer 1980). A substantial percentage of nonbreeders may occur in other permanently territorial, noncooperative species, with estimates of 35% in Carrion Crows (*Corvus corone*) in Scotland (Charles 1972, as cited by Patterson 1980) to 50% in the Rufous-collared Sparrow (Smith 1978). Cooperative species also show a wide range in the percentage of nonbreeders, from a low of 8% in one population of Bicolored Wren (*Campylorhynchus griseus*; Austad and Rabenold 1985), to 25% in Acorn Woodpeckers at Hastings (Koenig and Mumme 1987), and up to 80% in the African Yellow-billed Shrike (*Corvinella corvina*; Grimes 1980).

The percentage of nonbreeders (one year and older) averaged 31% for the Florida Scrub-Jay and 30% for the Mexican Jay, compared with an estimated 22% for scrub-jays at Hastings (Table 27) and perhaps 50% on Santa Cruz Island (data calculated from Atwood 1980b, Atwood et al. 1990).

Evidence that scrub-jays at Hastings may not acquire territories for several years includes: (1) the small proportion of territorial first-year females and males (10.7% and 4.9%, respectively, N = 223 breeding years; Table 12); (2) the percentage of jays banded as nestlings that eventually acquired territories on the study area (42% did so at age one, 33% at age two, and 25% at age three (Table 2); and (3) in four of five years, floaters were present in large numbers in March through early May and had no chance of breeding. Thus, noncooperative scrub-jays can have as high, or sometimes higher, proportions of nonbreeders than their cooperative relatives.

But is the "surplus" in noncooperative populations due to other factors besides habitat saturation? In Western Scrub-Jays, the sex ratio of floaters is roughly equal, simple pairs are the breeding unit, and lack of skill does not prevent young from acquiring territories and attempting to breed given the opportunity. More to the point, neither lack of mates or skill has any bearing on whether prebreeders delay dispersal or float. A lack of mates may prevent individuals from breeding but has no bearing on whether delayed dispersal or floating would be favored. Similarly, genetic or age effects ("skill") may deter individuals from attempting to set up territories and breed independently, but are unlikely to be important in determining whether delayed dispersal or floating is favored. However, in species where a critical group size is required for successful reproduction (e.g., *Campylorhynchus* wrens), breeding as part of a simple pair is not a viable option and delayed dispersal may be favored over floating.

Habitat differences

Brown (1974) originally predicted that permanently territorial cooperative breeders should inhabit mature stable vegetation types, but later acknowledged many exceptions

(Brown 1978). Of all the *Aphelocoma*, Western Scrub-Jays occupy the greatest geographic range and diversity of habitats (Pitelka 1951, Peterson and Vargas 1992). Florida Scrub-Jays occur in periodically burned oak scrub (Woolfenden and Fitzpatrick 1984) but may also inhabit fire suppressed and suburban landscapes that include oak scrub, although the latter may function in most years as population sinks (Breininger et al. 1995, 1996). Mexican Jays mostly inhabit mature oak-pine woodland, and Unicolored Jays are found in humid tall, luxuriant hardwood forest (Pitelka 1951, Webber and Brown 1994). Even on a local level, Western Scrub-Jays use a wider variety of habitats than their relatives. For example, where Mexican Jays and scrub-jays are sympatric, the latter use habitats that are rarely used by Mexican Jays. However, in similar habitats without Mexican Jays, scrub-jays expand into the former's preferred habitat (Marshall 1957; P. Stacey, pers. comm.). Burt and Peterson (1993) found that a cooperatively breeding population of scrub-jay in Oaxaca, Mexico, used a diverse assemblage of habitats and that conversion of its natural habitat has allowed expansion of the population.

Brown's (1974) generalization that cooperative breeders inhabit "mature, stable vegetation" followed from the idea that good quality habitat had to be saturated, so that the chance of a nonbreeder finding a good territory would be low. In contrast, Brown (1974: 73) suggested that "...the [western populations of] Scrub Jay inhabits a variety of habitats, including scrubby areas and chaparral, much of which is transient and created by forest fires. ...the higher reproductive rate and wider dispersal of the Scrub Jay may be viewed as adaptations for finding and exploiting newly available suitable habitat." The key idea is that some ecological factor acts to keep breeding habitat available or "unsaturated" in noncooperative breeders. As shown in the previous section, however, the large nonbreeding surplus in Western Scrub-Jays suggests that other factors are needed to explain the loss of delayed dispersal and group living.

THE MARGINAL HABITAT HYPOTHESIS

Koenig and Pitelka (1981) proposed that for group living to evolve in permanently territorial species, not only must high-quality habitat be saturated but marginal habitat must be relatively rare with a relatively sharp division between the two. Under these conditions, territories in high-quality habitat will be continuously occupied by established groups; those of intermediate quality will relatively rarely be occupied, and offspring will have a low probability of acquiring breeding status on a suitable territory. The key factor, however, is that because of a steep gradient between good and poor habitats, young individuals attempting to breed or even subsist in unoccupied habitat face a low probability of success and are "forced" to delay dispersal and remain on their natal territories.

If, however, a large proportion of intermediate and low-quality "marginal" habitat allows young individuals either to settle on territories, or float, early dispersal is favored. Predictions of the marginal habitat hypothesis (MHH) are contrasted with those of other models in Table 28, and examined below.

The MHH not only provides an ecological explanation for habitat saturation, it attempts to explain conditions that would preclude floating and favor delayed dispersal. Studies of cooperative breeders generally supported the MHH, including field experiments in which helpers actively competed for and filled artificially created breeding vacancies (Brown et al. 1982, Hannon et al. 1985, Pruett-Jones and Lewis 1990, Komdeur 1991). Prior studies of *Aphelocoma* also fit the predictions of the model. In the Island Scrub-Jay, Atwood (1980a) found breeding habitat "saturated" and floaters, including juveniles, only in "marginal" unoccupied habitat (open grassland with scattered shrubs or young trees and low *Baccharus* thickets that would be unsuitable for floaters on the mainland). In Florida, breeding space in high-quality habitat is always filled, and juveniles have a low probability of acquiring a territory. Juveniles do wander off their natal territories and are generally tolerated by unrelated adults until their post-juvenile molt in fall (Woolfenden and Fitzpatrick 1984). Group members, both breeders and helpers, then evict virtually all non-natal juveniles and older trespassers, and juveniles return to their natal territories and become helpers. Woolfenden and Fitzpatrick (1984; Fitzpatrick and Woolfenden 1986) demonstrate that jays breeding in marginal habitat have both lower survivorship and lower production of breeding age offspring, and therefore conclude that nonbreeding juveniles and adults would also experience low survivorship compared to staying on their natal territories.

Although these patterns support the MHH, evidence from the California Scrub-Jay does not. Nonbreeders, tolerated except during the height of the breeding season, used occupied territories and aggregated in habitats with the most abundant food resources. During the breeding season, breeders evicted floaters from their territories and floaters were rarely observed. In one year (1985) floaters were evicted only from the nest area and remained in the highest quality habitats, and microhabitat use and foraging behavior of floaters was identical to that of breeders. Thus, in the California Scrub-Jay, marginal or unoccupied habitat does not appear to be a factor in allowing nonbreeders to disperse and float. Tolerance of floaters by breeders and floaters' use of occupied habitat was also found in an study of *A. c. obscura* in southern California (M. J. Alpers, pers. comm.). This tolerance, in particular that of allowing nonbreeders access to territories but not to nests, is similar to the pattern in Florida Scrub-Jays and may be a relic behavior. In other territorial species, such as the Rufous-collared Sparrow (Smith 1978), floaters sneak through territories, which again suggests that floating does not depend on unoccupied or marginal areas for dispersal.

The MHH may explain higher levels of delayed dispersal and larger group sizes under different ecological conditions in cooperative breeders, but fails as a general explanation as to why another population is noncooperative (i.e., why nonbreeders float) for several reasons. The MHH predicts that the shape of the distribution in territory-habitat quality is fundamental. For example, Acorn Woodpecker territories at Hastings exhibit a steep territory-habitat gradient curve (little marginal habitat) and the birds are highly social

TABLE 28. Predictions of ecological models for the evolution of delayed dispersal, group living, and cooperative breeding (HS = Habitat Saturation[a]; MHH = Marginal Habitat Hypothesis[b]; FSJ = Florida Scrub-Jay Model[c]; EC = Ecological Constraints[d]; RCW = Red-cockaded Woodpecker Model[e]; BOP = Benefits of Philopatry[f]; WSJ=Western Scrub-Jays[g])

Predictions	HS	MHH	FSJ	EC	RCW	BOP	WSJ
Habitat saturated?	yes	yes	yes	yes	—	no	yes
Level of breeding constraints critical?	yes	no	yes	yes	yes	no	no
Floating ecologically constrained?	no	yes	yes	yes	no	no	no
Benefits of philopatry of primary importance?	yes	no	no	no	—	yes	no
Variance in rank order of territory quality	high	low	low	?	?	high	low

[a] Brown (1974, 1978, 1987).

[b] Koenig and Pitelka (1981), Koenig and Mumme (1987).

[c] Woolfenden and Fitzpatrick (1984), Fitzpatrick and Woolfenden (1986).

[d] Emlen (1982a).

[e] Walters et al. (1992b).

[f] Stacey and Ligon (1987, 1991).

[g] This study.

(Koenig and Mumme 1987); in New Mexico where a shallow gradient exists, group size is smaller. However, even in the latter, floating appears to be infrequent. Floating in cooperative breeders is usually rare (<5%; Woolfenden and Fitzpatrick 1984, Koenig and Mumme 1987, Brown 1987, Walters 1990). Further, Woolfenden and Fitzpatrick (1990) found nonbreeders "declining" available breeding space in high-quality habitat, and the presence of available but unused "suitable" territorial space in cooperative breeders is difficult to reconcile with a strict reading of the MHH (see also Stacey and Ligon 1991).

Under what habitat gradient (range of habitat conditions) is floating precluded? In Florida Scrub-Jays (Woolfenden and Fitzpatrick 1984), Acorn Woodpeckers in both California (Koenig and Mumme 1987) and New Mexico (Stacey and Ligon 1987), and other cooperative breeders (e.g., Grey-backed Shrikes, *Lanius excubitorius* [Zack and Ligon 1985b]), some unoccupied lower quality habitat is usually available. For example, Florida Scrub-Jays breeding in overgrown scrub fledge as many young as do unassisted pairs in high-quality habitat, although fledgling survival is lower in the former habitat due possibly to higher predation pressures (Woolfenden and Fitzpatrick 1984). If overgrown scrub can support successful breeding, floating should also be possible, although higher predation rates may also apply to floaters in this habitat (G. Woolfenden, pers. comm.). Indeed, nonbreeders in Florida do occasionally disperse into unoccupied habitats, forming small flocks that may persist for a month or two (Woolfenden and Fitzpatrick 1984).

Adults may force their offspring off territories even when marginal habitat may not be present. An extreme example is the Red Grouse (=Willow Ptarmigan, *Lagopus lagopus*), where nonbreeders are evicted from breeding habitats and are forced into areas where survivorship is so low that few survive through the winter (Watson and Moss 1970, Watson 1985).

Finally, the MHH also fails to explain how floating, and delayed dispersal and helping, could coexist as alternative strategies in the same population. In Purple Gallinules (*Gallinula martinica*), juveniles help but nonbreeding adults float in nonbreeding habitat (Hunter 1987). Young Green Jays (*Cyanocorax yncas*) in Texas delay dispersal for 15 months and assist their parents in defending the territory, but the nonbreeders are evicted after the next year's offspring are fledged (Gayou 1986) and evidently float until a vacancy is located. White-throated Magpie-Jay males disperse and a substantial number may float in unoccupied habitat, whereas most females are philopatric (Innes and Johnston 1996, Langen 1996b). In a population of western American Crows, Caffrey (1992) found that nonbreeders could delay dispersal, float, or switch between the two. The best documented example is the Australian Magpie (Carrick 1963, 1972; Veltman 1989), where some nonbreeders float in nonbreeding habitat and others remain on group territories.

THE FLORIDA SCRUB-JAY MODEL

Woolfenden and Fitzpatrick (1984, Fitzpatrick and Woolfenden 1986) developed a demographic model for the evolution of cooperative breeding in the Florida Scrub-Jay and the other *Aphelocoma*. Three variables are crucial to their model: D_0, the probability that early dispersers will become established successfully as breeders; B, the summed annual probabilities that a surviving helper remaining on its natal territory will encounter or create a breeding vacancy it can successfully fill; and L_h, the survival rate of a helper at home. The model predicts that as B and L_h increase, relative to early dispersal, delayed breeding and group living will be favored so long as D_o is low, even without any indirect fitness benefits (Table 28). In the Florida Scrub-Jay, D_o is low (high constraints on independent breeding); L_h is high (in comparison to that estimated for early dispersants floating in marginal overgrown scrub or sneaking through hostile occupied territories); and B is large, for males at least, due to territorial budding (Woolfenden and Fitzpatrick 1984).

Because the model does not include floating as an option, it assumes that nearly all Western Scrub-Jays breed as yearlings. Woolfenden and Fitzpatrick (1984:339) predict that D_o values for Western Scrub-Jays are high enough to favor early dispersal: "a wide range of acceptable habitats means that dispersing juveniles need only to stay alive in order to be more or less certain of obtaining space in which to breed as yearlings." D_o values, estimated from life-table variables, provide an index of breeding space competition (see Fitzpatrick and Woolfenden 1986). Similar D_o estimates for California, Island, and Florida scrub-jays, and for other taxa (Table 29) suggest that the level of breeding constraints per se is not sufficient to explain why one population is cooperative and another noncooperative; in fact, the level of breeding constraints provides absolutely no clue as to a population's social organization. More meaningful comparisons in D_o values could be made using fledgling production from simple pairs only; the added increment in fledgling production of breeders attributable to helpers may be important in the maintenance of delayed dispersal and cooperative breeding, but these secondarily derived benefits should not be used to assess the importance of breeding constraints leading to its evolution. When D_o is calculated for pairs only, this lowers the values for cooperative breeders, further blurring any relationship between breeding constraints and breeding system (Table 29).

L_h (adult helper-survivorship) and B (probability of a helper acquiring a breeding vacancy), on the other hand, may be much different between Florida and Western scrub-jays; unfortunately, both are impossible to measure for noncooperative species. Woolfenden and Fitzpatrick (1984, 1990) present a convincing argument why L_h may be relatively high compared to early dispersal in Florida. However, in California the converse may be true because jays can float, or even settle temporarily, in high-quality, occupied habitats as well as float and merely move through marginal ones. B (the summed annual probability of finding or creating a breeding vacancy) for Western Scrub-Jays, as for female Florida Scrub-Jays (which do not benefit from territorial budding, rarely inherit territories, and disperse farther), is even harder to evaluate; however, an increase in B in Florida Scrub-Jays must be a secondarily derived benefit of group living, rather than a primary casual factor.

The Florida Scrub-Jay model overemphasizes the importance of breeding constraints in the evolution of delayed dispersal, but provides valuable insight into the role of relative survivorship of nonbreeders pursing different strategies and other demographic factors. However, it falls short in its application to noncooperative populations simply because the model considers only two options for young birds: (1) disperse and breed, or (2) stay and delay breeding. The third option, floating, is not considered.

Walters et al. (1992a) applied a similar demographic model to empirical data from Red-cockaded Woodpeckers to evaluate fitness payoffs of young males that "depart and search" (DAS) for territories and those that "stay and foray"(SAF); all females employ the former strategy. Of males surviving to age one, 31% employed the DAS strategy and of these 39% became breeders on territories; 56% were solitary on territories and an estimated 5% remained as floaters. Walters et al. estimate that mean fitness for males

TABLE 29. INDEX OF BREEDING SPACE COMPETITION[a] FOR NONCOOPERATIVE CALIFORNIA AND ISLAND SCRUB-JAYS, COOPERATIVE FLORIDA SCRUB-JAYS, AND TWO OTHER COOPERATIVE BREEDERS

	Breeding space competition		
Species	Sex	Overall (with helpers)	Pairs only
Scrub-Jay			
California	Male	—	0.31 (0.23)[b]
	Female	—	0.54 (0.43)
Island	Both	—	0.07[c]
Florida	Both	0.27	0.44[d]
Acorn Woodpeckers	Male	0.08	0.09[e]
	Female	0.21	0.25
Green Woodhoopoes	Male	1.10	5.30[f]
	Female	0.43	0.92

[a] Lower values indicate higher levels of competition; a value of 0.1 would mean one breeding vacancy for every 9 nonbreeders.

[b] Values for breeder, juvenile, and adult nonbreeder survivorship as used in life tables (Table 23 and 24), where adult nonbreeder survivorship is 10% less than that of breeders; values in parenthesis are assuming nonbreeder survivorship equals breeder survivorship.

[c] Value calculated assuming 94% breeder survivorship (Atwood et al. 1990), adult nonbreeder survivorship 20% less than breeder survivorship, and juvenile survivorship and fecundity the same as for the Hastings population.

[d] Calculated from data in Woolfenden and Fitzpatrick (1984).

[e] Calculated from data in Koenig and Mumme (1987).

[f] Calculated from data in Ligon and Ligon (1978) and Ligon (1981).

employing the two strategies is nearly equal even without indirect fitness benefits as the potential advantage of early reproduction in DAS is balanced by a low probability of successful dispersal and increased survival in those adopting SAF. Walters et al. identify four variables that may be responsible for a reduced payoff in DAS relative to noncooperative species: (1) a high survivorship in males adopting SAF compared to birds in noncooperative species; (2) a low probability of surviving DAS birds attaining breeding status; (3) poor performance of males that do attain breeding status at a young age; and (4) a striking increase in reproductive success with age. These variables are nearly identical to those identified by Emlen (1982:32) as the key factors in favoring delayed dispersal and that "Such situations are expected to be rare, and philopatry (remaining at home) should occur only when the option of early personal reproduction is severely constrained." As noted before, these attributes were shown to differ little between cooperative and noncooperative *Aphelocoma*.

THE BENEFITS OF PHILOPATRY MODEL

Stacey and Ligon (1987) developed a model for the evolution of cooperative breeding in Acorn Woodpeckers that they term the benefits of philopatry (BOP) model. Based on their long-term study of Acorn Woodpeckers in New Mexico, they concluded that, contrary to previous models (Table 28), all suitable habitats are not saturated and no sharp gradient exists between good and poor habitats. Accordingly, nonbreeders remain on high-quality territories because helping for up to three years, and then breeding on a high-quality territory, accrues higher LRS than early dispersal and independent breeding on a territory of lower quality.

Similar results, albeit with a different interpretation, were found by Fitzpatrick and Woolfenden (1988) and Fitzpatrick et al. (1989). Analyses of life-time reproductive success in Florida Scrub-Jays indicate that the highest LRS is achieved by breeding as early as possible on a suitable territory; success in acquiring a territory at an early age is, together with breeder life-span, the most important contributor to a jay's lifetime reproductive success. However, when lifetime fitness is compared for Florida Scrub-Jays breeding in different habitats, they found that jays could delay breeding for several years in the good habitat and still have higher fitness than early breeders in the poor habitat (overgrown scrub). Thus, in both Florida Scrub-Jays and Acorn Woodpeckers, individuals that breed early in the always available but less suitable habitats will have lower life-time fitness than individuals delaying dispersal but eventually breeding on better territories, assuming the choice of a territory is final and permanent. Fitzpatrick and Woolfenden see this as a high cost of early dispersal, whereas Stacey and Ligon see it as a high benefit of philopatry (i.e., opposite sides of the same coin). Interestingly, when Fitzpatrick et al. (1989) examined how the production of breeding descendants varied within high-quality habitat, profound differences became evident; some areas showed much higher production of breeding descendants than others. Although this may result from differences in individual (genetic) quality, if it is due to long-term differences in habitat, then high-quality habitats are passed down through families, resulting in high variation in the success of different lineages (Brown 1974, Fitzpatrick et al. 1989). Such variation in habitat quality would lend support to the variance hypothesis and some of Brown's predictions (Table 28). However, Fitzpatrick et al. (1989) could find no evidence that individuals differentially compete for these areas, a necessary requisite for the BOP model.

Stacey and Ligon (1991; see also Waser 1988, Powell 1989) propose that natal philopatry is favored when a high and stable variance exists in territory quality, and/or group size affects the quality of a breeding opportunity. Under the BOP hypothesis, young in small groups on high-quality territories should delay dispersal in anticipation of inheriting breeding space, whereas young born into very large groups or on low-quality territories should disperse and breed as soon as possible. If group size is critical, nonbreeders should remain only in groups of some critical mass that assures the groups of high reproductive success and survivorship. For example, in *Campylorhynchus* wrens (Rabenold 1984, 1985; Austad and Rabenold 1985, Zack and Rabenold 1989), reproductive success of pairs is near zero and increases with group size so that reproductive output (per capita) peaks in groups of either three (*C. griseus*) or four (*C. nuchalis*). In these species, nonbreeders are effectively prevented from independent breeding by high nest predation rates, and neither habitat saturation nor differences in territory quality are implicated (Austad and Rabenold 1985). Under these conditions, floating is not precluded, but the advantages of group living and helping for nonbreeders make floating, or even breeding in simple pairs, a poor alternative.

The BOP model predicts that young in noncooperative species should disperse at independence either because: (1) the habitat is more uniform and territories are of similar quality; (2) interterritory quality fluctuates unpredictably over time (therefore high-quality territories are not "inheritable"); or (3) individuals do not benefit from living in groups.

Despite such clear examples of species that may form groups because of "group-living effects," two problems exist with this suggestion. First, the BOP hypothesis does not clearly distinguish between primary and secondary group-living effects. For example, Stacey and Ligon (1991) suggest that Florida Scrub-Jays and other cooperatively breeding New World jays delay dispersal because of anti-predator benefits of group living. The orchestrated sentinel system (McGowan and Woolfenden 1989) and other group behaviors in Florida Scrub-Jays may lessen predation; pairs with helpers do experience lower nest predation rates (Schaub et al. 1992). Another group-living effect is territorial expansion with increased group size in Florida Scrub-Jays. This not only lessens any adverse impact from resource depression, but allows for territorial "budding," which Woolfenden and Fitzpatrick (1984) identify as an important factor in maintaining cooperative breeding in the Florida population. Such secondarily derived benefits may be substantive but cannot be attributed as a primary cause of delayed dispersal, although they may be important in its maintenance (current utility). Because it is always possible to point to some benefit of group living, one cannot suggest that another population is noncooperative because group benefits do not apply.

Other predictions of the BOP concern how variance in territory quality differs among populations that vary in social behavior. To date, tests have involved comparisons between widely separated populations of cooperative species (e.g., Acorn woodpeckers in California and New Mexico; Koenig and Mumme 1987, Stacey and Ligon 1987). A more appropriate test can be between the closely related Western and Florida scrub-jays. Scrub-jay territories at Hastings were ranked from Type 1 to Type 3 on the basis of occupancy rate and vegetation characteristics. Of approximately 45 territories (range of 40 to 52 over the study period), five (~11%) were of very low quality. In Florida, the quality of the habitat depends on whether it has been burned recently, but all of the area in the periodically burned scrub is continuously occupied in nearly all years (therefore Type 1 and Type 2 territories). Fledgling production over the study area at Hastings also appears to be more variable than in Florida. In Figure 40, both the Hastings and Florida study areas are arbitrarily divided into 9 parts. Within high-quality habitat, fledgling production is relatively uniform in Florida, ranging from 1.9 to 2.2 (Woolfenden and Fitzpatrick 1984), whereas in California it ranged from 0.6 to 1.4.

While this suggests greater variance in territory and habitat quality in the noncooperative population, it could be argued that the "marginal" unburned, overgrown scrub in Florida should be included, despite the fact that unburned scrub is rarely colonized but rather "grows up" and eventually takes over what was formerly high-quality habitat. Stacey and Ligon (1991) suggest that comparisons of high- and low-quality habitat in Florida would reveal marked variation in habitat-territory quality, implying that this would run counter to both the Florida Scrub-Jay model (Woolfenden and Fitzpatrick's 1984) and the MHH (Koenig and Pitelka 1981). However, one could argue that this difference is exactly the basis for the latter model (a steep drop-off in quality in rarely occupied, marginal habitats). The fact that these low-quality habitats are not continuously "saturated" only refutes Koenig and Pitelka and Woolfenden and Fitzpatrick to the extent one stretches the definition of "suitability," and once again illustrates the problem in defining "suitable" and "marginal" habitats (see also Koenig et al. 1992). In a study of Florida Scrub-Jays at the Kennedy Space Center, where habitat is generally more marginal, Breininger et al. (1995) found that some areas acted as source populations and others as population sinks. All areas may appear "saturated," but only because of immigration from source habitats. Over a three-year period, demographic performance was related to landscape features; as at Archbold, open scrub oak was higher quality habitat, but territories also included a matrix of low-quality and unsuitable habitat.

According to the BOP, a shortcoming of prior analyses is that they compared habitat, not territory, quality (Stacey and Ligon 1991). For delayed dispersal to be favored under the BOP, high-quality territories must be inheritable, i.e., long-term differences in quality on a per-territory basis. Early dispersal will occur in situations with low variance in territory quality, which can arise either by very low correlation and large differences in quality among years, or high correlation but uniform quality among years. For example,

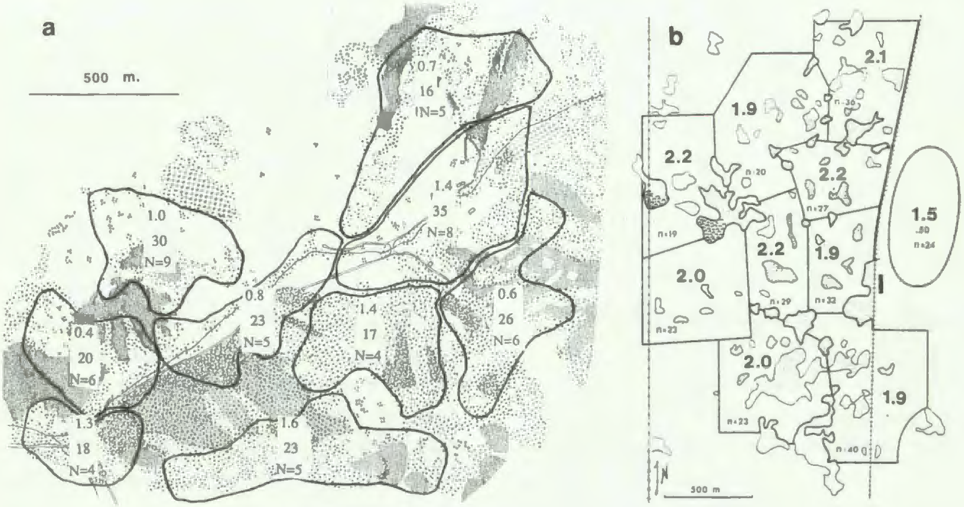

FIGURE 40. Variation in fledgling production over nine randomly drawn geographic segments of the California and Florida scrub-jay study areas. (a) California Scrub-Jay study area at the Hastings Reservation, (b) Florida Scrub-Jay study area at the Archbold Biological Station (from Woolfenden and Fitzpatrick 1984). Numbers are overall mean fledgling production calculated by averaging mean fledgling production for all breeding pairs (or family groups) on each territory in each area; N = breeding-pair years in each area.

Waser (1988), in relating philopatry to variance in home range quality, hypothesized that the banner-tailed kangaroo rat (*Dipodmys spectabilis*) dispersed, despite all other conditions favoring philopatry, because no correlation existed between home range quality among years.

However, as with defining "marginal habitat" under the MHH, it is not clear how much or little variance is required to favor one social system over another. Also, interterritory comparisons among cooperative and noncooperative species are difficult to make for several reasons. Because territories are occupied and defended by groups in cooperative species, and better territories are more continuously occupied by larger groups, this may result in more stable boundaries and greater permanence of groups on higher quality territories, and combines (and confounds) group effects with effects of territory quality. In noncooperative populations, because only pairs occupy territories, no group effects occur and territory boundaries often fluctuate upon the death of one of the breeders. The BOP model also assumes that the choice of a territory is permanent. However, movements in noncooperative breeders from low-quality to higher quality habitat may be common (e.g., Great Tits, *Parus major* [Krebs 1971]; Eurasian Magpies [Baeyens 1981]). At Hastings, 20% of all territory vacancies were filled by breeders changing territories. This suggests that young nonbreeders are able to breed initially in low or intermediate quality habitat and later acquire a better site. In cooperative breeders, on the other hand, young that disperse to low-quality habitats may not be able to shift back because nondispersing individuals are present to fill vacancies on territories in high-quality habitats. A third problem involves scale; the MHH generally examines habitat gradients over a wide geographic area, whereas BOP focuses on interterritory differences within a small, local area.

DELAYED DISPERSAL THRESHOLD MODEL

None of the models (Table 28) are fully supported by comparisons among the cooperative and noncooperative *Aphelocoma*. Most treat only two options (disperse and breed or stay and delay breeding) and sidestep the question of floating. In populations where floaters are restricted to the same degree as helpers from independent breeding, the relevant comparisons are between early dispersal (and floating) vs. delayed dispersal (and helping), not between delayed dispersal and independent breeding. The Delayed Dispersal Threshold Model (Koenig et al. 1992) addressed some of the short comings of the previous models by giving equal treatment to early dispersal and floating, delayed dispersal and helping, and independent breeding. Rather than specific predictions, the model provides a general guide for organizing and evaluating the relative importance of ecological factors under which the different dispersal strategies, including floating, are favored. The model lists 13 factors influencing the dispersal options available to offspring, most of which have been discussed in the context of the other models. Here, I focus closely on how three factors—resource depression on territories, habitat available for floating, and habitat variability—influence dispersal options in *Aphelocoma* jays and show why floating is the preferred option in Western Scrub-Jays.

Resource depression on territories

Models developed by Waser (1981, 1988) and Brown (1982, 1987) explore the relationship of territory quality and resource depression to group living. If territories have limited resources or low rates of resource renewal, the addition of individuals beyond the breeding pair may lower survival and reproductive success to such a degree that breeders should evict offspring, or offspring should choose to leave, or both. Where resource renewal is slow, group size may be limited to pairs despite other factors favoring retention of offspring. Nonbreeders may, however, increase the fitness of breeders by helping to defend the territory, or by helping to raise young. These secondarily derived benefits may lower the absolute costs to breeders of allowing offspring to remain. Lowered defense costs were used by Brown (1969) to explain why adults would tolerate young in Mexican Jays and other cooperative breeders. In contrast, on high-quality territories, specifically those with rapid resource renewal or those with "nondepreciable resources" (Waser 1988), additional group members will have relatively little effect on survival and reproductive success.

Does resource depression explain the different patterns of territorial behavior, dispersal, and group living in *Aphelocoma* jays? Both territory size and habitat productivity contribute to resource levels, but data on the latter are scant. Comparisons of territory size suggest that on large territories resource levels are lower per unit area, more patchy, or fluctuate more strongly. In this context, it is noteworthy that in Florida, scrub-jay territories are extremely large (mean of 7.2 ha for pairs and increasing significantly with group size; Woolfenden and Fitzpatrick 1984) compared to those recorded for Western Scrub-Jays (1.5 to 2.5 ha). Mexican Jay territories in Arizona are extremely large (20 to 25 ha), support large groups (ranging from 5 to 22 jays), but territory size apparently does not fluctuate with group size (Brown 1987, Brown et al. 1997). Brown (1987) suggested that Mexican Jay territories are larger than needed except at peak densities, but data are lacking, particularly with respect to winter conditions. Unicolor Jay territories may be even larger; the one territory Webber and Brown (1994) were able to map in its entirety ranged between 41 and 45 ha, and was held by a group of six.

Several lines of evidence suggest that territories in Western Scrub-Jays are not of such low quality as to preclude group living. First, breeders at Hastings tolerated their own young and unrelated floaters in the nonbreeding season and, in 1985, even in the breeding season. Second, Western Scrub-Jays occupy habitats that support group-living Mexican Jays when the latter are absent. Third, acorns, an important resource for *Aphelocoma* jays, are unlikely to limit group size because they are a "time-limited" resource (Waser 1988); processes other than consumption by scrub-jays limit their availability. Acorns remain on oaks for several months and numerous seed cachers and seed predators remove acorns before and after seed fall. In most years, acorns are superabundant with respect to a jay's (or an aggregation of jays) ability to eat or cache them, and this decreases the cost of sharing a territory either with related offspring or unrelated floaters. Little information on insect productivity is available for comparison, but nestling starvation in Florida Scrub-Jays is extremely low, and adults (with helpers) foraged only 40% of daylight hours during the breeding season. Nestling starvation averaged 17% at Hastings and breeders foraged 70% of daylight hours, suggesting potential for resource depression effects. Additional work on food resources of these jays would be required to provide a definitive answer regarding the importance of resource depression on their dispersal options (see also Burt 1996).

Habitat available for floating

In some cooperative species, special features of their habitat can strengthen ties of helpers to home groups. For example, roost-holes in Green Woodhoopoes (*Phoeniculus purpureus*; Ligon 1988) and granaries in Acorn Woodpeckers (Koenig and Mumme 1987) appear to be critical for breeders and nonbreeders alike; when limited, offspring that either attempt to set up a territory or float will do poorly. When the critical resource is important only for breeding (e.g., nest cavities), this does not constrain floating, and some other explanation for delayed dispersal must be invoked. When breeding space itself is in some way limited, as has been suggested for the cooperative *Aphelocoma* jays, it is more difficult to pin-point the resources that make space or other habitat features critical for nonbreeders. However, a complete theory for group living in any species must include an explanation of what ecological factors make adjacent habitat unsuitable for floating by nonbreeders.

Access to high-quality habitat should result in high floater survivorship, but actual floater survivorship is unknown. Data on relative age-specific survivorship of juveniles, adult nonbreeders, and territorial jays are particularly crucial for resolving questions concerning the costs and benefits of floating. In many cooperatively breeding species, nonbreeding helpers have higher survivorship than breeders (e.g., male Florida Scrub-Jays [Woolfenden and Fitzpatrick 1984], Acorn Woodpeckers [Koenig and Mumme 1987]). In contrast, nonbreeder survivorship in noncooperative species is thought to be lower than that of breeders, due to risks of dispersal (Brown 1974, Emlen 1982), being forced into marginal habitats (Watson 1985), or not having the benefits of unrestricted access to critical resources and microhabitats (Ekman and Askenmo 1984). However, Ekman and Askenmo (1986) found that nonbreeding adult male Willow Tits (*Parus montanus*) had higher survivorship than adult male breeders.

In *Aphelocoma* jays, the types of habitat available to nonbreeders are strongly influenced by the territorial behavior of breeders. In Florida Scrub-Jays, juveniles wander and are tolerated on all territories prior to their post-juvenile molt (Woolfenden and

Fitzpatrick 1984). Later, however, they are not tolerated on non-natal territories, and either return to their natal territories (the preferred option), or move to unoccupied areas, usually non-breeding habitats. Survivorship of helpers does not stabilize at adult breeder levels until age two, but this seems to be caused primarily by the risks of dispersal forays (Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1988). Nonbreeders in Florida must trespass occupied, hostile territories in search of breeding vacancies, or float in unoccupied habitats with high predation rates (Woolfenden and Fitzpatrick 1984, 1990) and possibly also a paucity of acorns.

At Hastings, scrub-jay breeders tolerated both offspring and unrelated floaters of all ages on their territories except in May and June, and the floaters aggregated primarily where acorns were in good supply. Most remained sedentary throughout the winter and early spring, storing and recovering acorns as did the resident territorial breeders. By late April in most years, aggregations dissolved and floaters were rarely seen until early July when some of the same individuals returned and joined independent juveniles. Their disappearance coincided with increased aggression by territorial jays, but they also disappeared from areas unoccupied by breeders. In all months but May and June, floaters had unrestricted access to the best habitats, aggregated in loose flocks, and did not invest time and energy in territory defense or reproduction, and it is possible that their survivorship may be near (or even exceed) that of breeders.

In contrast, juvenile Island Scrub-Jays move to unoccupied areas by early August as breeders aggressively exclude them, including their own offspring, from their territories (Atwood 1980a; J. Atwood, pers. comm.). Yet, they do well, even though they must encroach on territories to gain access to acorns (Atwood 1980a). Few details are available on dispersal in Mexican Jays, but young retain juvenile characteristics for several years (Brown 1963), which may extend the period of tolerance and lessen the aggression of adults (Lawton and Lawton 1986). Degree of sociality varies within the range of the Mexican Jay (Brown and Brown 1990); they occur primarily in montane oak-woodland, but no obvious habitat or vegetation feature(s), separate high- and low-quality habitats, either for breeders or potential floaters (Edwards 1986).

Habitat variability

It is necessary to attempt to separate variability on a per-territory basis from phenomena that occur on a larger scale. For example, at Hastings, territory quality (occupancy rate) was correlated with vegetation characteristics, including the number of oak species and area of oak canopy. Both of these variables are indicators of reliable acorn production on a per territory basis. Hence, on the local scale, territory quality is predictable and the relative ranking of territories probably does not vary greatly from year to year. However, on a broader regional scale in California, acorn production is highly variable and strongly affects scrub-jay population density and dispersal options. This may be a key point in the secondary loss of cooperation in Western Scrub-Jays.

Acorn production in high-quality scrub-jay habitat in Florida shows little annual and spatial variation relative to that in California. In Florida, scrub oaks form continuous, shrub-like stands covering many hectares, and each scrub oak produces few seeds. Estimated production on the average territory was 128,000 acorns, and ranged from 14,000 to 331,000 (DeGange et al. 1989). Group size ranges from 2 to 10 jays in Florida, and each jay eats and caches approximately 8,700 acorns per year. It seems probable that 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-