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THE EVOLUTION OF DELAYED DISPERSAL
IN COOPERATIVE BREEDERS

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ABSTRACT

   Why do the young of cooperative breeders — species in which more than two individuals help raise offspring at a single nest — delay dispersal and live in groups? Answering this deceptively simple question involves examining the costs and benefits of three alternative strategies: (1) dispersal and attempting to breed, (2) dispersal and floating, and (3) delayed dispersal and helping. If, all other things being equal, the fitness of individuals that delay dispersal is greater than the fitness of individuals that disperse and breed on their own, intrinsic benefits are paramount to the current maintenance of delayed dispersal. Intrinsic benefits are directly due to living with others and may include enhanced foraging efficiency and reduced susceptibility to predation. However, if individuals that disperse and attempt to breed in high-quality habitat achieve the highest fitness, extrinsic constraints on the ability of offspring to obtain such high-quality breeding opportunities force offspring to either delay dispersal or float.
   The relevant constraint to independent reproduction has frequently been termed habitat saturation. This concept, of itself, fails to explain the evolution of delayed dispersal. Instead, we propose the

delayed-dispersal threshold model as a guide for organizing and evaluating the ecological factors potentially responsible for this phenomenon. We identify five parameters critical to the probability of delayed dispersal: relative population density, the fitness differential between early dispersal/ breeding and delayed dispersal, the observed or hypothetical fitness of floaters, the distribution of territory quality, and spatiotemporal environmental variability.

A key conclusion from the model is that no one factor by itself causes delayed dispersal and cooperative breeding. However, a difference in the dispersal patterns between two closely related species or populations (or between individuals in the same population in different years) may be attributable to one or a small set of factors. Much remains to be done to pinpoint the relative importance of different ecological factors in promoting delayed dispersal. This is underscored by our current inability to explain satisfactorily several patterns including the relative significance of flooting, geographic biases in the incidence of cooperative breeding, sexual asymmetries in delayed dispersal, the relationship between delayed dispersal leading to helping behavior and cooperative polygamy, and the rarity of the co-occurrence of helpers and floaters within the same population.

Advances in this field remain to be made along several fronts. In particular, we advocate experimental tests of specific ecological factors affecting the parameters of the delayed-dispersal threshold model, studies of noncooperatively breeding taxa focusing on what constraints to independent reproduction exist and why they do not result in delayed dispersal, and studies of intraspecific variation in group size and composition of cooperative breeders in relation to local habitat gradients and patchiness.

INTRODUCTION

COOPERATIVE, or communal, breeding occurs when more than a pair of individuals exhibit parent-like ("helping") behavior toward young of a single nest or brood. Numerous variations have been identified, including helping at the nest by offspring that delay dispersal and remain with their parents, and various forms of cooperative polygamy or plural breeding in which more than a single male or female share breeding status within the same social unit. Reported sporadically in the early 1900s, cooperative breeding was first reviewed by Skutch (1935, 1961), whose extensive experience in the neotropics exposed him to avian social behavior found only rarely in temperate areas. The recent explosion of work in this field stems largely from the theoretical revolution inspired by Hamilton's (1964) theory of kin selection and the evolution of social behavior combined with the advent of color-banding, which allowed workers to follow individuals throughout their lives. Today, cooperative breeding in birds, mammals and even fishes garners considerable attention in behavioral research. Several excellent reviews exist, most recently those of Brown (1987), Emlen (1991), and the collection of papers in Stacey and Koenig (1990).

Many early discussions of cooperative breeding confound the evolution of delayed dispersal and group living with the evolution of helping behavior per se. Historically, two features justify this coupling. First, delayed dispersal and helping behavior usually co-occur. Second, the beneficial fitness consequences of helping may also be a major selective benefit for delayed dispersal (Rabenold, 1984; Stacey and Ligon, 1991). However, numerous exceptions to the first of these features are now known. Delayed dispersal, for example, is often not associated with cooperative polygamy, a phenomenon that may be more common than once thought (e.g., Rabenold et al., 1990). Furthermore, even within systems in which nonbreeders delay dispersal, subsequent helping behavior is not universal [e.g., green jays *Cyanocorax yncas* in southern Texas (Gayou, 1986) and Australian magpies *Gymnorhina tibicen* (Veltman, 1989)], and may frequently be characteristic of only some offspring [e.g., the northwestern crow *Corvus caurinus* (Verbeek and Butler, 1981)]. It is therefore important to distinguish the questions of delayed dispersal and group living from why, once in groups, auxiliaries may subsequently help raise offspring not their own.

The latter of these questions has generated considerable controversy over at least two issues: What is the relative importance of kinship to the evolution of helping behavior? And, is helping behavior an unselected consequence of group living? Valuable discussions of the first of these are provided in the reviews cited above and in Emlen and Wrege (1989), while the possibility that helping behavior is an unselected trait is discussed at length by

Jamieson and Craig (1987) and Jamieson (1989, 1991), who have advocated this concept, and by Ligon and Stacey (1989, 1991), Koenig and Mumme (1990), and Emlen et al. (1991), who have argued against it on various counts.

Until recently, the question of why young of many cooperative breeders delay dispersal and live in groups has generated considerably less controversy: with few exceptions, authors have endorsed the concepts of "habitat saturation" or "ecological constraints" (Emlen, 1982a). In the years since Emlen's (1982a) paper, however, this apparent consensus has been repeatedly challenged. Recently, for example, Stacey and Ligon (1987, 1991) and Zack (1990) criticized both the validity and the logical basis of habitat saturation, proposing in its stead their own hypotheses stressing the benefits of philopatry.

Our purpose here is to present a new, inclusive framework for understanding the evolution of delayed dispersal. Because it has dominated much of the thinking in this field, we focus on nonbreeding helpers at the nest, individuals that have delayed dispersal and independent reproduction and provide aid to offspring not their own. Aid generally consists of feeding nestlings or fledglings, but can also include incubation and nest defense. Most of our discussion will focus on birds, primarily because avian studies have played a preeminent role in this field. The ideas discussed, however, are equally applicable to cooperatively breeding mammals and fishes, recently reviewed by Gittleman (1985) and Taborsky and Limberger (1981), respectively, and in some cases eusocial insects (Andersson, 1984).

We begin with a historical review and critique of habitat saturation. The review reflects our personal biases and is not comprehensive. We present it here to aid in the understanding of the current controversy and to provide an alternative to the perspective of Brown (1987, 1989) on the origin and history of ideas in this field. We then present the delayed-dispersal threshold model, which we offer as a conceptual successor to habitat saturation.

HABITAT SATURATION

Historial Background

The first person to develop a concise hypothesis to explain delayed dispersal and group living in cooperative breeders was Selander (1964) in his monograph on *Campylorhynchus* wrens, a largely tropical genus containing several cooperative species. Selander (1964: 206) wrote:

> Under [conditions of consistently high habitat occupancy], a young, inexperienced bird dispersing from the parental territory might have little chance of establishing an adequate territory and breeding. Possibly there would be greater advantage to the individual, in terms of total reproductive success, in delaying reproduction and remaining on the parental home area on the chance that the parental territory or an adjacent area with which the bird was familiar would become available. Chances for survival presumably would be greater and, by serving as a helper, the young bird would gain experience in parental activities which could enhance reproductive success later in life.

This passage is notable for several reasons. First, it clearly separates delayed dispersal and group living from helping behavior. Most aspects of what has since become known as the habitat saturation hypothesis are formulated to explain delayed dispersal. Selander also provides a suggestion for the advantages helpers might gain by helping. [Written contemporaneously with Hamilton's (1964) paper on kinship and inclusive fitness, and in the absence of data on relatedness, it is not surprising that the benefits proposed by Selander pertained to the direct (sensu Brown, 1980), rather than indirect, fitness of helpers.] The possibility that territory quality may play an important role in determining the costs and benefits of delayed dispersal is presented, as is the potential importance of inexperience on the part of young individuals and the possibility that nondispersers will someday inherit their natal territory or at least breed nearby. There is the implicit recognition that helpers are better off obtaining a reproductive opportunity on their own, either on their natal territory or nearby, if and when they can. Selander (1964), however, identifies few specifics as to the ecological conditions that might favor delayed dispersal and group living other than to suggest elsewhere that they might arise under conditions of relatively low, constant adult mortality rates such as are presumably characteristic of "stable" tropical and subtropical areas.

A second notable contribution is the discussion of the adaptive significance of territoriality in birds by Brown (1969a,b). Brown devised a model that divided the potential effects of territorial behavior into three levels depending on population density. In level 1, the density is low and all individuals are able to breed in their preferred habitat. In level 2, the density is higher and some individuals are forced to breed in less productive habitats. Finally, in level 3, "all habitats where breeding could possibly occur are occupied by territorial individuals, and a *surplus* of potential breeders exists as non-breeding *floaters*" (Brown, 1969a: 294, emphasis in the original). Such surplus individuals may behave in a variety of ways, one of which is to remain in their natal groups as nonbreeding helpers. Brown proposes that this might occur if the population surplus is particularly large, in which case "the probability of an individual's eventually gaining the opportunity of successful breeding . . . may be greater if it remains within the family group awaiting the demise of its elders . . . than if it forsakes all claims to its old territory and attempts to establish a new one in the face of uniformly fierce defense" (p. 316).

Brown's (1969a) model, which was not specifically designed to represent cooperative breeding systems, differed subtly but importantly from the earlier one of Selander (1964). In particular, Brown was interested in a simple system in which a species bred in two distinct territory types and thus did not address the importance of territory quality to delayed dispersal. Rather, he suggested that level-3 densities arise only when all habitats where breeding *could possibly* occur are occupied; in this way it is more extreme than Selander's (1964) formulation of the same idea. Like Selander (1964), however, Brown (1969a) offered no indication of the specific conditions that might make delayed dispersal a superior route to eventual breeding other than the "uniformly fierce defense" offspring must overcome owing to the large population surplus present under level-3 conditions.

An hypothesis for what specific conditions might apply to cooperative breeders was finally provided by Verbeek (1973) in his monograph on the yellow-billed magpie (*Pica nuttalli*). Although this species is not a cooper-ative breeder, it displays strong sociality in both breeding and nonbreeding seasons. He devotes a section to a comparative discussion of social systems in corvids and specifically attempts to explain group living in gray-breasted (Mexican) jays (*Aphelocoma ultramarina*) and non-group-living in western scrub jays (*A. coerulescens*). Verbeek (1973: 50) concludes that the habitat requirements of the gray-breasted jay are narrower and that "whereas yearling Scrub Jays, because of the wider habitat range of the species, successfully exist in marginal habitats, the [Gray-breasted] Jay presumably makes limited use of marginal habitats, because it probably does not favor the survival of yearlings." He even presents (p. 48) a flow diagram of the possible routes to sociality in corvids, an idea (and figure) also developed by Brown (1974).

Whereas prior workers suggested only the demographic conditions under which delayed dispersal in cooperative breeders might be advantageous, Verbeek went beyond this by proposing a set of ecological circumstances that might lead to those demographic conditions, specifically, a narrow ecological tolerance limiting the availability of marginal habitat to young birds. In so doing, Verbeek's model focused directly on the factors potentially constraining the alternative of floating as well as dispersal and independent breeding, and thus allowed for the possibility of significant constraints to independent reproduction in both cooperative and noncooperative species.

Subsequent theoretical papers published in the 1970s reiterated Selander (1964) and Brown's (1969a) ideas concerning the demographic correlates of cooperative breeding. Ricklefs (1975), for example, developed the idea that cooperative breeding occurs when a high juvenile recruitment to adult mortality ratio leads to intense competition for space. Brown (1974) summarized a variety of ideas concerning the demographic causes and consequences of cooperative breeding, many of which have held up well with subsequent work (see Brown, 1987). Brown (1974), however, did not elaborate on the ecological factors leading to those demographic conditions other than repeating the hypothesis that cooperative breeders should inhabit "stable, climax vegetation forms" (p. 73). He did, how-

ever, suggest that increased productivity of groups with helpers is not likely to explain the evolution of cooperative breeding. Instead, Brown proposed that helping behavior increases fitness only under the specialized conditions of "intense competition in a population that is always at or near carrying capacity" (p. 77). Although partly a repetition of Selander (1964), an important feature of this statement is the explicit recognition that intrinsic advantages are unlikely to provide a general answer to why cooperative breeders live in groups.

Besides these largely theoretical contributions, initial publications from several important long-term studies of cooperative breeders became available in the period 1965–1975. This empirical work made possible major reviews by Brown (1978), Emlen (1978), and Gaston (1978). Gaston (1978) discussed mostly the potential costs and benefits of helping, and like most other authors failed to provide any ecological context for delayed dispersal other than mentioning the apparent correlation with warm climates and, like Ricklefs (1975), emphasizing the importance of a demographic situation in which there is relatively high adult survivorship and thus few vacant territories. Brown (1978) discussed at length the life history traits of cooperative breeders and reiterated the demographic correlates of this behavior, again providing no ecological context other than to abandon the suggestion that it is associated with stable and climax environments. Emlen (1978), in contrast, maintained support for the hypothesis that cooperative breeding is associated with stable environments. He also discussed the hypothesis that cooperative breeding occurs when "suitable habitat becomes filled or 'saturated'" (p. 250), a situation which he referred to as habitat saturation.

The calculations made by Brown (1975, 1978) and Emlen (1978) comparing the relative fitness contributions of a bird that delays dispersal to one that disperses and attempts to breed on its own were particularly notable. Despite including the effects of both group living and helping behavior, these calculations proved inconsistent: they correctly predicted helping in the superb blue fairy-wren (*Malurus cyaneus*) and among yearling Tasmanian native hens (*Gallinula [Tribonyx] mor-*

tierii), but failed to do so for Florida scrub jays, where the fitness payoff to independent breeding always outweighed those of helping. Emlen (1978: 257) concluded: "we should predict that non-breeding scrub jays will cease being helpers *whenever* they can successfully compete for a vacancy left by the disappearance of a previously breeding individual" (emphasis in the original).

This conclusion is a clear statement of the hypothesis that, all other things being equal, the fitness of nonbreeders delaying dispersal and helping is lower than what they would experience if they successfully dispersed to a territory capable of supporting breeding and bred independently. Why, then, do these nonbreeders not disperse and breed independently? The answer is that all other things are *not* equal; in particular, dispersal and independent breeding is apparently constrained due to the demographic conditions already known by this time as habitat saturation (e.g., Stacey, 1979a).

The alternative to this habitat saturation hypothesis is that nonbreeders experience higher lifetime fitness by delaying dispersal and helping than by attempting to breed independently at an early age because of the intrinsic advantages of the former alternative. This idea surfaces regularly in earlier works. For example, Rowley (1965: 291) concluded for superb blue fairy-wrens that "the presence of supernumeraries in the family group shortens the frequency of the breeding cycle to the irreducible minimum occupied by the incubation and nestling stages and must therefore be regarded as a highly efficient adaptation to a widely varying climate, by a multi-brooded species." Similarly, Brown (1963), in an early publication on gray-breasted jays, stated "Teleologically, it would appear that the advantages to the individual [Gray-breasted] Jay of reserving a territory for himself are outweighed by the advantages gained through flock membership" (p. 151). He goes on to list three advantages that might be gained by individuals in groups: the acquisition of a better territory, increased foraging efficiency, and reduced predation.

Although various benefits to delayed dispersal and group membership continued to be identified between 1979 and 1984, considerable evidence began accumulating for

the importance of the habitat saturation hypothesis (e.g., Stacey, 1979a; Atwood, 1980; Koenig, 1981a; Woolfenden and Fitzpatrick, 1984). We note two theoretical developments during this period. First, Koenig and Pitelka (1981) extending the hypothesis proposed by Verbeek (1973), developed a graphical model of habitat saturation that we call the "marginal habitat hypothesis." This hypothesis, discussed in greater detail below, postulated a high proportion of "optimal" versus "marginal" habitats leading to a situation in which most marginal habitats would generally be occupied by individuals excluded from high-quality territories. Few habitats of marginal quality would then be available for occupancy by either potential breeders or floaters, leading to relatively low fitness by individuals choosing either of those alternatives.

A second important development was that of Emlen (1982a; see also Orians et al., 1977), who pointed out the analogy between the usual perception of habitat saturation leading to restricted breeding options by offspring, and conditions where the cost of rearing young is prohibitive owing to adverse conditions. In both cases breeding options are restricted, but in the latter situation independent breeding is constrained not by the lack of a suitable territory, but by the inability of some individuals to acquire the requisite resources for breeding other than space. With the "skill hypothesis" (see below) Brown (1985, 1987) expanded this idea to any situation in which differential experience causes an energy threshold for successful breeding to be exceeded by some individuals and not others. Species constrained by space include those living under apparently stable ecological conditions in which habitat saturation has generally been invoked to explain delayed dispersal, while species constrained by the high cost of rearing young include those living under highly variable conditions in which at least some pairs appear to be unable to breed by themselves, independent of territory quality. Emlen (1982a) subsumed both possibilities under an ecological constraints model. In order to distinguish the two situations, we refer to the former, in which individuals do not directly benefit by the presence of others, as extrinsic constraints and the latter, in which

the benefits accruing to grouped individuals lead to delayed dispersal, as intrinsic benefits.

These and other papers helped forge a consensus for the importance of ecological constraints to the evolution of delayed dispersal. The consensus was short-lived, however, being broken soon by the models of Wiley and Rabenold (1984), Stacey and Ligon (1987, 1991), Waser (1988), and Zack (1990), and by apparently contradictory data presented by Zack and Ligon (1985b), Stacey and Ligon (1987), and McCallum et al. (in press). In general, these alternative models stress the potential advantages to delayed dispersal (Heinsohn et al., 1990). They have often been advanced as alternatives to ecological constraints, but the precise ways in which this is true have not always been clear, for reasons discussed below. Currently we believe it is fair to say that there is more confusion than agreement concerning the role of ecological constraints and habitat saturation to the evolution of delayed dispersal and cooperative breeding.

Critique of Habitat Saturation

The cause of this confusion lies squarely with the use of the term habitat saturation. Habitat saturation has no generally accepted definition and has been used in at least three overlapping contexts. First, it is frequently used to refer to population size relative to resources, that is, to relative density (e.g., Stacey and Ligon, 1987; Jones et al., 1988). In this sense, habitat saturation is a continuous variable that is only meaningful when defined relative to another population (Zack and Ligon, 1985a). Second, it is used in a general sense to describe a syndrome of intense competition over territories that are rarely vacant (Emlen, 1991; Walters et al., in press). In this form, habitat saturation encompasses several hypotheses concerned with the specific ecological conditions leading to the demographic conditions that in turn select for delayed dispersal and cooperative breeding (Walters et al., in press). Third, some authors have used habitat saturation to refer to one specific set of possible ecological conditions leading to intense competition over territories; that is, to only a subset of the general syndrome just referred to above. This more specific defini-

tion can be particularly troublesome, since authors rejecting habitat saturation are often doing so only for one possible form of the more general syndrome, not for the general syndrome itself.

Consequently, we recommend that the term habitat saturation be used only when it is explicitly defined by the user; however, this is not the only difficulty with this concept as an explanation for delayed dispersal and helping behavior. As used by most authors, habitat saturation is not a sufficient explanation for delayed dispersal for at least the following three general reasons.

Ambiguity. Selander (1964) defined the conditions now known as habitat saturation as those in which young have little chance of establishing an "adequate territory and breeding." What, however, is an "adequate" territory?

A territory that is adequate (or other similarly vague labels, such as a suitable, successful, optimal, or marginal) could be defined on an absolute, if arbitrary, basis. For example, an optimal territory might reasonably be defined as one in which, on average, reproductive success and survivorship are sufficient for inhabitants to replace themselves, while a marginal territory might be one in which inhabitants cannot expect to do so. Applying such a criterion, however, tells us little about the preferred dispersal strategy for individual offspring, which will depend on the quality of the territories to which they can disperse relative to that of their natal territory. For example, because the benefits of remaining on the natal territory and helping to raise related offspring will correlate with the number of offspring raised and hence most likely be related to territory quality, the minimally acceptable territory to which an individual born on a high-quality territory might disperse will be of higher quality than that for an individual born on a low-quality territory (see below). Indeed, what constitutes an acceptable territory, and thus whether or not the habitat is perceived as being saturated, may very well differ for every individual.

Offspring can always disperse and occupy space somewhere; the question is not whether any unoccupied habitat exists, but under what conditions the available unoccupied

habitat is so poor that delayed dispersal becomes a preferable alternative. The view that habitat saturation means that individuals are forced to remain in their natal groups because *no* unoccupied habitat of whatever quality exists (e.g., Zack, 1990; Ligon et al., 1991) has never been part of the concept of habitat saturation, at least as envisioned by Selander (1964), Verbeek (1973), or Koenig and Pitelka (1981).

Habitat heterogeneity and the scale of assessment. In any nondeclining population, the number of potential recruits produced over the long term must at least equal, and will usually exceed, the number of available vacancies, at least in high-quality habitat. Thus, most territorial populations will frequently exist, at least in some subset of their range, under conditions of habitat saturation in which breeding territories are limited (Koenig and Mumme, 1987; Heinsohn et al., 1990; Emlen, 1991). At least two consequences follow.

First, habitat saturation is insufficient to explain delayed dispersal and helping behavior. Hunter (1987), for example, found that limited availability of suitable breeding habitat in the purple gallinule *Porphyrula martinica* led to floating rather than helping by yearlings even though juveniles regularly acted as helpers, and Carmen (in press) found that the level of demographic constraints may be identical among cooperative and noncooperative populations of scrub jays. It follows that habitat saturation, although possibly necessary, is not sufficient to distinguish species in which young delay dispersal from those in which they do not (Stacey and Ligon, 1987; Heinsohn et al., 1990; Zack, 1990; Emlen, 1991).

Second, the scale at which habitat saturation is assessed is critical: within a single homogeneous habitat of high quality, habitat saturation is quite likely, whereas habitat saturation is unlikely at the level of a large population spread out over many habitats of variable quality. Within any specified habitat, saturation can be defined as occurring when the number of competitors is greater than the number of suitable territories (Brown, 1987: 71). By definition, high-quality habitats will generally fulfill these conditions while low-quality habitats will not. Unfortunately, we are left with the nontrivial problem of distin-

guishing different habitats. We are further burdened with the even more difficult problem of assessing available resources, which in turn determines the potential "number of suitable territories" within any particular habitat.

For these reasons, we believe that the emphasis on the demographic correlates of cooperative breeding espoused by numerous authors, epitomized by the use of the term habitat saturation in the general form discussed above, has been misplaced. Many cooperative breeders live at relatively high densities and under conditions in which young birds have a difficult time obtaining reproductive vacancies, but so do many noncooperatively breeding species. The critical difference, rather than being the existence of a population surplus and consequent competition for space, is that this surplus consists of offspring that delay dispersal and remain on their natal territories rather than pursuing some alternative strategy such as floating.

Circularity. The concept of habitat saturation entails an element of circularity: Does it result in reduced dispersal or vice versa (Wiley and Rabenold, 1984; Austad and Rabenold, 1986; Stacey and Ligon, 1987; Zack, 1990)? Stacey and Ligon (1987), for example, argued that delayed dispersal has been selected for by various intrinsic benefits and that habitat saturation is a result, not a cause, of reduced dispersal. Heinsohn et al. (1990) suggested a similar possibility based on the likelihood that most cooperative breeders have been studied in preferred habitats, thus biasing our view of the relationship between habitat saturation and cooperative breeding. This criticism highlights the difficulty that there is generally no independent means of assessing habitat saturation other than measuring the extent to which individuals do not disperse and establish independent territories when we, as observers, think they should or could do so.

THE DELAYED-DISPERSAL THRESHOLD MODEL

These difficulties with the concept of habitat saturation prompt us to advocate a more general framework for the evolution of delayed dispersal in cooperative breeders, which we call the "delayed-dispersal threshold model." The model is a generalization of that presented by Koenig and Pitelka (1981) and is analogous to the well-known polygyny threshold model of Verner and Willson (1966) and Orians (1969). Various factors influencing optimal group size in a similar model have been discussed by Brown (1982, 1987); other authors who have presented models in the context of delayed dispersal or joint-nesting include Gowaty (1981), Waser (1988), Powell (1989), and S. Zack and B. J. Stutchbury (pers. commun.). Our model focuses on the ecological factors leading to differing dispersal patterns of individuals compared either inter- or intraspecifically.

The basic model is presented in Figure 1, where "habitat fitness" or "territory quality" (Emlen, 1991) gradients are graphed. They are obtained by plotting the fitness state of individuals pursuing a particular strategy on the y-axis. Fitness or fitness states for an individual (ego) are functions of several parameters, including (1) ego's reproductive success and survivorship, (2) the reproductive success and survivorship of kin due to ego's help (or hindrance), (3) the quality of the habitat or territory on which ego lives, and (4) the contingent probability of switching to other fitness states in the future as would happen when, for example, a floater or helper obtains a territory in high-quality breeding habitat. Parameters (1) and (2) correspond to the individual's future direct and indirect fitness effects (Brown, 1980), and are generally easiest to envision as measured relative to individuals of comparable age engaged in other fitness states. With respect to (3), the complete range of available environments is ranked in order from worst to best (based on their quality for breeding) on the x-axis. This results in monotonically increasing curves starting with "nonhabitat," where the hypothetical fitness of an individual is zero, to the best available habitats, where fitness is relatively high. Parameter (4) indicates that fitness is not measured instantaneously, but includes a time dimension incorporating the probability of future successful reproduction, given that ego is currently engaged in a particular strategy. Thus, at any point in time, an individual behaving optimally will attempt to pursue the option yielding the highest fitness state.

The first option, represented by W_d, is ego's fitness if it delays dispersal and remains on its
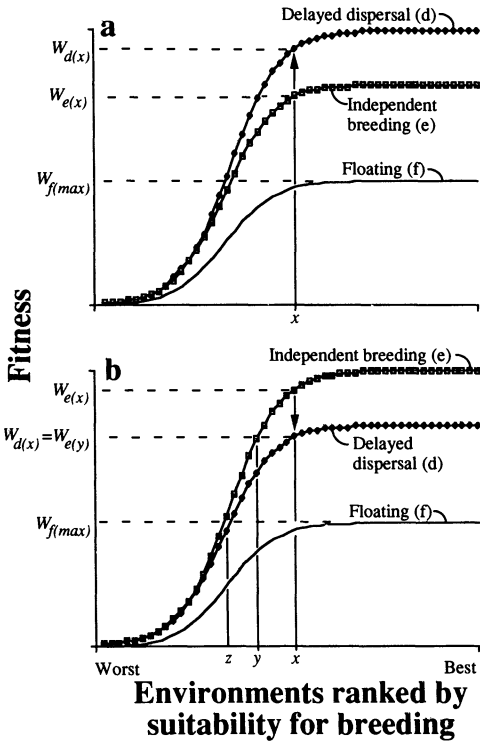
FIG. 1.   THE DELAYED DISPERSAL
          THRESHOLD MODEL.

The habitat fitness or territory quality gradient for a population is obtained by ranking territories from worst to best on the abscissa, while graphing the fitness of occupants on those territories on the ordinate. Gradients can be derived for individuals pursuing alternative strategies. Territory quality gradients for individuals dispersing and breeding (W_e), delaying dispersal (W_d), and floating (W_f) are plotted here. The values for each of these depend on the quality of the environment (x) on which the individual lives. (a) Delayed dispersal yields higher fitness than either dispersing and breeding on a territory of comparable quality or floating, even in the best available habitat, i.e., $W_{d(x)} > W_{e(x)}$ and $W_{d(x)} > W_{f(max)}$, where $W_{f(max)}$ is the fitness of floaters in the best available habitat for floating. (b) Delayed dispersal yields lower fitness than dispersing and breeding on a territory of comparable quality but higher fitness than floating, i.e., $W_{e(x)} > W_{d(x)} > W_{f(max)}$. In this case, individuals are forced to delay dispersal because of extrinsic constraints.

natal territory, during which time it delays breeding (henceforth "delayed dispersal/helping"). The second, represented by W_e, is ego's fitness if it disperses, settles on the best avail-

able territory and attempts to breed (henceforth "dispersal/breeding"). The third, represented by W_f, is its fitness if it disperses but becomes a floater that is not breeding for whatever reason (henceforth "dispersal/floating"). Note that while neither floaters nor helpers presumably reproduce while engaged in these options, both strategies may yield high fitness states by augmenting survivorship and future successful reproduction; in addition, helpers may facilitate the reproduction and survivorship of relatives. Also, although the model focuses on the options available to newly independent offspring, it is not limited to this stage and can also be applied to individuals at later stages in their lives, as long as comparisons are made with other individuals of similar age and status.

For all three strategies, an individual's fitness is dependent on the quality of the territory on which it lives; this is represented by the parenthesized subscript. Thus, the fitness of an individual remaining on territory x as a nonbreeder is $W_{d(x)}$ [Fig. 1(a)]. This is a probabilistic value that averages the fitness of all individuals engaged in this option relative to those pursuing alternative options. The fitness of an individual that attempts to breed on territory x is $W_{e(x)}$. Finally, the fitness of a floater that occupies habitat x is $W_{f(x)}$. As with the other options, the fitness of floaters depends on the quality of the habitat available to them; under certain circumstances, all floaters may be able to occupy the best available areas [designated by $W_{f(max)}$], perhaps by sneaking in interstices of high-quality territories, while under other circumstances, they may be excluded from high-quality areas and forced to float in inferior habitats. Territories are ranked according to their quality for breeding. This ranking will usually, but not necessarily, be highly correlated with their quality as habitat for floaters.

The distinction between intrinsic benefits and extrinsic constraints currently maintaining delayed dispersal and group living in this model corresponds to the situations depicted in Figures 1(a) and 1(b), respectively. In Figure 1(a), $W_e < W_d$ for all environments, and thus an individual's fitness is greater if it delays dispersal and helps on its natal territory than if it disperses and breeds on a territory of the same quality as that on which it was

born; this corresponds to the situation in which intrinsic benefits are sufficient to maintain delayed dispersal (see below). In constrast, Figure 1(b) shows the situation in which extrinsic constraints are the proximate factor driving delayed dispersal and group living; in this case, $W_e > W_d$ for all environments.

Consider an individual born on territory x [Fig. 1(b)]. If it disperses and floats and is able to occupy the best available habitat, it experiences fitness $W_{f(max)}$. If it delays dispersal and remains a nonbreeder on its natal territory, it experiences fitness $W_{d(x)}$. Finally, if it disperses and breeds, it chooses the best available territory from those in which vacancies exist (say y) and experiences fitness $W_{e(y)}$.

Which of these three options yields the greatest fitness depends by definition on the relative values of $W_{f(max)}$, $W_{d(x)}$, and $W_{e(y)}$. In the example shown in Figure 1(a), the intrinsic benefits of delayed dispersal and group living are so great that, assuming the natal territory to be of reasonably high quality (which is quite likely, since high-quality territories by definition yield the majority of offspring), this option is superior not only to dispersal/floating but to dispersal/breeding, even on the best available territory. In Figure 1(b), territories x and y have been chosen so that $W_{d(x)} = W_{e(y)}$; thus, if the best territory available is of higher quality than y, an offspring should disperse and breed independently on that territory, while if it is of lower quality than y, it should delay dispersal/help on its natal territory. Floating in this example is unlikely for any offspring, since only in the event that a bird is born on a territory of quality lower than z and there was no vacant territory of higher quality, would a bird be better off floating than delaying dispersal. For the offspring born on territory x, dispersing/floating, even in the best habitat, yields lower fitness than delaying dispersal and remaining on territory x as a nonbreeder. This need not be the case; indeed, the widespread existence of floaters indicates that $W_{f(max)} > W_d$ in many cases. In most of the examples we discuss, however, $W_{f(max)}$ is set unrealistically low so as to allow us to focus on the differences between W_e and W_d.

Since nonbreeding helpers are likely to have survivorship at least as high as breeders

(Woolfenden and Fitzpatrick, 1984; Koenig and Mumme, 1987; Rabenold, 1990), the fitness differential between $W_{e(x)}$ and $W_{d(x)}$ is essentially the cost of delayed reproduction. The fitness differential between $W_{e(x)}$ and $W_{f(max)}$ is the cost of delayed reproduction and the additional cost (if any) owing to lower survivorship of floaters compared to helpers.

Assumptions of the Model

Here we discuss several assumptions relevant to the delayed-dispersal threshold model. These assumptions are difficult to test and, like those relevant to the polygyny threshold model (Davies, 1989), are unlikely to be met in many, if not most, realistic situations. Most of the assumptions, however, can be relaxed without jeopardizing the model's usefulness; this is done in the subsequent discussion.

Relationship between territory quality and fitness. Territories or habitats must vary in quality in ways that directly influence the fitness of inhabitants. The most likely reason this might not be true is because of spatiotemporal environmental variation (discussed below; see also Powell, 1989). If great enough, such variation may all but obliterate a correlation in quality of a given territory among years, thereby eliminating any correlation between territory quality over the long term and fitness. For example, this was apparently the case for the banner-tailed kangaroo rats (*Dipodomys spectabilis*) studied by Waser (1988), in which young dispersed despite meeting all of the expected preconditions for philopatry.

Perfect knowledge. Individuals are assumed to have perfect knowledge of both the existence of vacancies and the quality of territories or habitats in which vacancies exist, even prior to their departure from the natal territory, and thus are able to choose the best dispersal alternative at any point in time. This assumption is dependent on the extent to which individuals examine available territories and are able to accurately discriminate among them prior to and during potential dispersal events. Some of the meager information currently available on these behaviors is discussed on pages 124 and 129.

Ideal-free settlement. Individuals are free to settle where their expected fitness is greatest. Because of behavioral constraints such as incest avoidance (e.g., Koenig and Pitelka,

1979), this may not always be true, although relatively few data are available to assess the importance of such constraints in any species.

Irrevocability of decision. In its simplist form, the model assumes that the choice of a breeding territory is permanent. Territory switching, however, is readily accommodated by envisioning the model to represent probabilistic "fitness states" rather than lifetime fitness. That is, once an individual chooses a territory, it can expect to accrue fitness at a certain rate. This rate is based not only on its expected survivorship and reproductive success on that territory, but also on the degree to which that territory provides opportunities for the owners to later move to a higher-quality territory, or the degree to which it may expose the owners to the possibility of a decline in resource value forcing desertion and dispersal in search of a new, more adequate territory elsewhere.

Several prior models (e.g., Fitzpatrick and Woolfenden, 1986; Stacey and Ligon, 1987; S. Zack and B. J. Stutchbury, pers. commun.) explicitly assume that the choice of a breeding territory is permanent. Such inflexibility is certainly not general. For example, secondary dispersal by breeders, including the return to their natal group as nonbreeding helpers after having dispersed and bred elsewhere, is common among Californian acorn woodpeckers (Koenig and Mumme, 1987), and extensive territory switching has been documented in both the red-cockaded woodpecker (Walters, 1990) and the noncooperatively breeding western scrub jay (Carmen, in press). Depending on the degree of such flexibility, the option pursued by an individual at any particular time will be a function of the relative quality of territories and expected payoffs of the relevant options at that time and correspondingly less on long-term mean territory quality.

Dispersal options are distinct. The model assumes that the ultimate goal of a nonbreeder is to become a successful breeder, and that both delayed dispersal and floating are potential means to this end. Determination of the preferred options therefore requires consideration of three alternatives: (1) dispersal to the best available territory or habitat where independent breeding is at least a possibility, (2) dispersal and floating until a vacancy in an acceptable territory can be filled, thereby including possible failure to settle and breed in the first and perhaps additional breeding seasons, and (3) delayed dispersal and remaining on the natal territory as a nonbreeder.

Two definitions are helpful. First, dispersal is the process of permanently leaving the natal territory. Once an individual disperses, it can either settle on a territory where breeding can be attempted or become a floater. Second, floating designates the behavior of nonterritorial and nonbreeding individuals that have left their natal territory. Floating is neither a simple nor uniform phenomenon; rather, it is part of a continuum of space-use behaviors that grade into forays made by territorial individuals in search of reproductive opportunities (see below). In particular, note that the traditional view that floaters are necessarily individuals lacking site fidelity is wrong. Instead, floaters frequently employ site-specific tactics leading to future access to breeding opportunities (Smith, 1978; Smith and Arcese, 1989; P. Arcese, pers. commun.; S. Zack and B. J. Stutchbury, pers. commun.; see below).

The model generally assumes that the three dispersal options of delayed dispersal/helping, dispersal/breeding, and dispersal/floating, are qualitatively distinct. However, not only may individuals switch back and forth between options, but each may grade into the others in some species. For example, species such as Galápagos mockingbirds *Nesomimus parvulus* (Curry and Grant, 1990) and western bluebirds *Sialia mexicana* (J. L. Dickinson, pers. commun.) include individuals that simultaneously help at one nest while breeding at another. Similarly, individuals that delay dispersal and help may simultaneously spend a significant amount of time foraying in search of vacancies, at least at some seasons (Woolfenden and Fitzpatrick, 1986; Hooge, 1992). Such behavior is tantamount to floating, with the distinction that individuals have a home base to which they can return when and if needed. Finally, although floaters are generally assumed to be nonbreeders, it is possible, although as yet unsubstantiated, that they may occasionally egg dump (females) or obtain extrapair copulations (EPCs, males), thereby blurring the distinction between dispersal/floating and dispersal/breeding. We

know relatively little about the extent, much less the significance, of such potential complexities.

Furthermore, ours is not the only way in which to structure the alternatives available to offspring. For example, Brown (1987: 103–104), Zack (1990), and Walters et al. (1992) consider two dispersal alternatives instead of three and contrast delayed dispersal ("stay and foray") with dispersal ("depart and search"). One rationale for this is that floating and independent reproduction are simply different outcomes of the single strategy of early dispersal; in other words, an individual disperses and then either finds an acceptable vacant territory, settles, and subsequently attempts to breed, or continues to float. Although this may be true, we prefer to separate these latter two alternatives in order to emphasize the range of options potentially available to an individual during a particular breeding season (see also Brown, 1987: 96–97).

Point of view and potential conflict. The dispersal strategy of an offspring can be examined from either the point of view of the offspring itself or that of the breeding group members (usually parents) to whose group it belongs. The interests of these two sets of individuals are not always concordant, and conflicts can be expected between them (e.g., Emlen, 1982b; Vehrencamp, 1983; Koenig et al., 1988). Following prior treatments, we assume that parents or other group members cannot force offspring to delay dispersal, but that they can evict offspring if it is in their own best interest. Thus, just as there may be constraints on the ability of offspring to obtain high-quality breeding territories, there may be constraints on their ability to delay dispersal and help, depending on the real or hypothetical consequences of such an action on the remaining group members. Parental tolerance of nondispersal is likely, however, because parents will usually benefit from the retention of offspring beyond the point at which delayed dispersal is beneficial to the offspring themselves (Emlen, 1982b). This prompts us here to take the point of view of the offspring rather than the parents. Constraints that may be imposed by conflicts of interest with other group members are subsumed under the conditions, discussed below, influencing the dispersal options of offspring.

Several authors have proposed an alternative view that conflict is usually absent between parents and offspring and that delayed dispersal represents a form of "parental facilitation" (Brown and Brown, 1984) or extended parental care (Ligon, 1981; Fitzpatrick and Woolfenden, 1986; Ligon and Ligon, 1988). Overt conflict between parents and offspring involving persistence of the latter in groups, however, can sometimes be directly observed (e.g., Hannon et al., 1987; Koenig et al., 1988), indicating that conflict does exist, at least under some circumstances. Furthermore, the fact that yearlings and older offspring have higher reproductive value than eggs or nestlings, cited by Fitzpatrick and Woolfenden (1986: 154) as a reason for a lack of parent-offspring conflict and offspring retention, is a demographic fact true for all species and cannot, in and of itself, be sufficient to explain these phenomena. Instead, the costs and benefits accruing to both breeders and offspring as a consequence of differing dispersal strategies are important in determining which option is pursued (e.g., Orians et al., 1977; Emlen, 1982b).

Delayed Dispersal: Intrinsic Benefits or Extrinsic Constraints?

As shown by the contrast of Figures 1(a) and 1(b), there is a dichotomy in the potential causes for delayed dispersal and group living. First, there may be intrinsic benefits to delayed dispersal and group living such that individuals achieve higher lifetime fitness by delaying dispersal compared to either attempting to breed independently or floating, all other things being equal. Two major ecological reasons why this might be true are lowered predation and increased foraging efficiency (Alexander, 1974). Alternatively, the intrinsic benefits promoting delayed dispersal and group living may not outweigh the costs, in which case the lifetime fitness of individuals that delay dispersal will be lower than that of those dispersing early and attempting to breed independently, all other things being equal. In this latter situation, grouped individuals do not gain because of the presence of others, but rather gain "solely from the presence of some other resource in the environment" (Alexander, 1974: 329); in other words, they are ecologically forced to live in groups

in order to have access to a critical resource (see also Altmann, 1974; Walters et al., in press). Such individuals are "making the best of a bad job" and gain by group living only in comparison to living without access to the critical resource, not by the presence of other individuals per se. In principle, at least, identification of the critical resource is straightforward: If the constraint is removed, young will disperse. Mates and breeding space (territories) are likely candidates for resources that might be limited and act in this way.

The distinction between intrinsic benefits and extrinsic constraints can only be applied at the level of current functional utility and not at the level of evolutionary origin (sensu Tinbergen, 1963; see also Sherman, 1988). For example, even if a population is forced into group living due to extrinsic constraints, individuals may still reap secondary benefits from living in groups (see below). These secondary benefits can be expected to coevolve with delayed dispersal and group living (Creel and Creel, 1991), eventually leading to a situation in which secondary benefits of group living might exceed the fitness loss due to delayed dispersal. At that point, individuals in the population will appear, on a proximate level, to delay dispersal and live in groups because of intrinsic benefits, even though delayed dispersal originated as a consequence of extrinsic constraints. Thus, the distinction between these two routes to delayed dispersal and cooperative breeding may, at least in some cases, be primarily historical.

Because of this problem, it will almost always be more profitable to ask whether intrinsic benefits or extrinsic constraints are currently exercising greater control over delayed dispersal rather than to attempt to reject one or the other hypothesis as playing some role in any particular system. Documentation of significant fitness benefits to delayed dispersal constitutes the primary evidence for the importance of intrinsic benefits, whereas documentation of constraints to dispersal is the primary evidence for the importance of extrinsic constraints.

Both routes to delayed dispersal involve ecological constraints; the distinction between them is in the nature rather than the presence of a constraint to independent breeding. The two routes correspond to the two major types of ecological constraints identified by Emlen (1982a): Habitat saturation and a biased sex ratio are extrinsic constraints to independent breeding, whereas if independent breeding is restricted because the cost of rearing young is prohibitive for some pairs, then delayed dispersal is a consequence of intrinsic benefits to group living. Cooperative breeders that are classically territorial are most likely to fit into the first of these categories, while those that are not are likely to fit into the second (Emlen, 1982a). Note that the term "intrinsic benefits" stresses the advantages to group living accruing via this route, but we could equally as well use the term "intrinsic constraints" to stress the limitation on independent breeding resulting from the high cost of rearing young by pairs or small groups.

Species in which intrinsic benefits appear to be particularly important include stripe-backed wrens *Campylorhynchus nuchalis*, where the ability of pairs and trios to deter predators and thus breed successfully is extremely low compared to larger groups (Rabenold, 1984), Harris's hawks *Parabuteo unicinctus*, in which cooperative hunting appears to be a crucial foraging strategy (Bednarz, 1988), and white-winged choughs *Corcorax melanorhamphos*, where the skills needed for independent reproduction apparently require several years to develop, and group living is virtually obligatory (Heinsohn et al., 1988; Heinsohn, 1991; see also below). Intrinsic benefits also are likely to be an important component of helping in cases in which helpers do not necessarily delay independent breeding, since helping in such species is a behavioral option chosen by individuals that might otherwise be putting additional time and effort into raising their own offspring. For example, as mentioned earlier, in Galápagos mockingbirds (Curry and Grant, 1990) and in western bluebirds (J. L. Dickinson, pers. commun.), some individuals act concurrently as helpers at one nest and as breeders at another. Perhaps the best studied species in this category is the white-fronted bee-eater *Merops bullockoides*, a species in which birds frequently switch between helping their parents and independent breeding. Emlen (1984, 1990) found considerable evidence that intrinsic benefits to group living are paramount to the decision to act as a helper: When environmental conditions were good, birds

tended to breed independently, but when conditions were poor, birds were more likely to be helpers, and breeders even competed for helpers. The benefits of helping in the years when conditions were poor was confirmed by the observation that helpers significantly increase, and in some years are required, for successful reproduction (Emlen, 1990).

There is equally compelling evidence for the importance of extrinsic constraints in a variety of cooperative breeders. For the Florida scrub jay, Woolfenden and Fitzpatrick (1984: 238), following the format of Brown (1975, 1978) and Emlen (1978), compared the expected fitness of individuals that delay dispersal and help with those that disperse early and breed. Similar to earlier results, Woolfenden and Fitzpatrick found that under all plausible circumstances the inclusive fitness of a young jay is strikingly greater if it disperses early and breeds than if it delays dispersal and helps. It follows that extrinsic constraints restrict the ability of offspring to pursue this superior dispersal option. This is further supported by the finding that individuals delaying dispersal appear to have lower survivorship and lifetime reproductive success than the apparently superior individuals that disperse and breed either in their first year or after a single season of helping (Fitzpatrick and Woolfenden, 1988).

Young, nonbreeding helper acorn woodpeckers in California spend considerable time and effort engaged in forays designed to locate potential reproductive vacancies (Hooge, 1992) and fight vigorously for the opportunity to abandon their status as helpers and to fill reproductive vacancies, as predicted if extrinsic constraints are paramount to promoting delayed dispersal (Koenig, 1981b; Hannon et al., 1985). There is also considerable evidence that the lifetime fitness of birds that delay dispersal is not greater than that of individuals that disperse early and breed, at least if the latter are able to settle on a high-quality territory (Koenig and Mumme 1987; Stacey and Ligon, 1987). Finally, Emlen (1984) tested the importance of ecological constraints to the evolution of delayed dispersal in this species indirectly by correlating the proportion of individuals delaying dispersal with the level of breeding constraints. He found that the proportion of helpers increased with fewer repro-

ductive vacancies. These data all fail to support the existence of significant intrinsic benefits to delayed dispersal; they are consistent with the hypothesis that extrinsic factors are important to the current maintenance of delayed dispersal in this species.

There is also experimental evidence for the importance of extrinsic constraints in several species. Pruett-Jones and Lewis (1990) removed breeding male superb blue fairy-wrens and found that virtually all nonbreeding helpers present in the population dispersed when sufficient reproductive vacancies were created, supporting the hypothesis that extrinsic constraints on reproductive opportunities, not intrinsic benefits to delayed dispersal and helping, caused these individuals to remain as nonbreeding helpers. An analogous experiment was conducted by Walters et al. (in press) by adding nesting and roosting cavities to areas previously unoccupied by red-cockaded woodpeckers. Most areas where cavities were added were subsequently occupied by birds that had previously been helpers or floaters, supporting the hypothesis that cavities are a critical, limited resource constraining early dispersal/breeding. Particularly compelling evidence is provided by Komdeur (1991) for the Seychelles brush warbler (*Acrocephalus sechellensis*). Komdeur created vacancies on the apparently saturated island of Cousin by transplanting individuals from 16 territories to the previously uninhabited island of Aride. Not only were all vacancies created on Cousin filled, sometimes within hours, by birds who had previously been helpers, but all 61 young produced by the transplanted birds on Aride dispersed and bred independently the following year. These examples yield strong evidence for delayed dispersal resulting primarily from extrinsic constraints on the availability of high-quality reproductive vacancies.

General Factors Affecting Delayed Dispersal

Five general demographic, ecological and environmental factors affect the decision to delay dispersal in the model: (1) relative population density, (2) the fitness differential between early dispersal/breeding and delayed dispersal, (3) fitness of floaters, (4) the distribution of territory quality, and (5) spatiotemporal environmental variability. We will consider each in turn.

1. Population density. Relative density could be the primary factor distinguishing the conditions leading to cooperative breeding. For example, assume that one population is limited during the nonbreeding season, and a second is limited during the breeding season. Under these conditions, the breeding population size of the second, but not the first, might be large relative to available high-quality territories, constraining the ability of offspring to disperse early and breed. Conditions leading to relatively low population density might be chronic or intermittent, depending on the variability of environmental conditions. This latter possibility is discussed below.

The contrast between populations with low and high relative density is shown in Figure 2, which depicts the options available to offspring given that extrinsic constraints provide the proximate impetus for delayed dispersal [as in Fig. 1(b)]. In the low-density situation [Fig. 2(a)], only a fraction of high-quality environments are occupied and y is the best available unoccupied territory, while in the high-density situation [Fig. 2(b)], all environments of moderate quality or higher are occupied and z is the best available unoccupied territory.

If the density is low, an individual born on the highest-quality territory x should disperse and breed independently, since $W_{e(y)} > W_{d(x)} > W_{f(max)}$ [Fig. 2(a)]. If the density is high, $W_{d(x)} > W_{e(z)} > W_{f(max)}$ [Fig. 2(b)]; hence, the same individual would experience highest fitness if it remains as a nonbreeder on its natal territory.

We have drawn the W_f gradients identically in the two parts of Figure 2. It is likely, however, that increased breeder density might interact with W_f by forcing floaters into less than the best habitats. Thus, population density may affect the relative desirability of delayed dispersal by determining, in part, the quality of the territories available to offspring that disperse and either float or attempt to breed.

A review of the factors potentially influencing population density is beyond the scope of this paper; the important point is that all such factors may influence delayed dispersal as shown in Figure 2. As discussed above, relative density is equivalent to the degree of habitat saturation as used by some authors. When used in this context, habitat saturation does

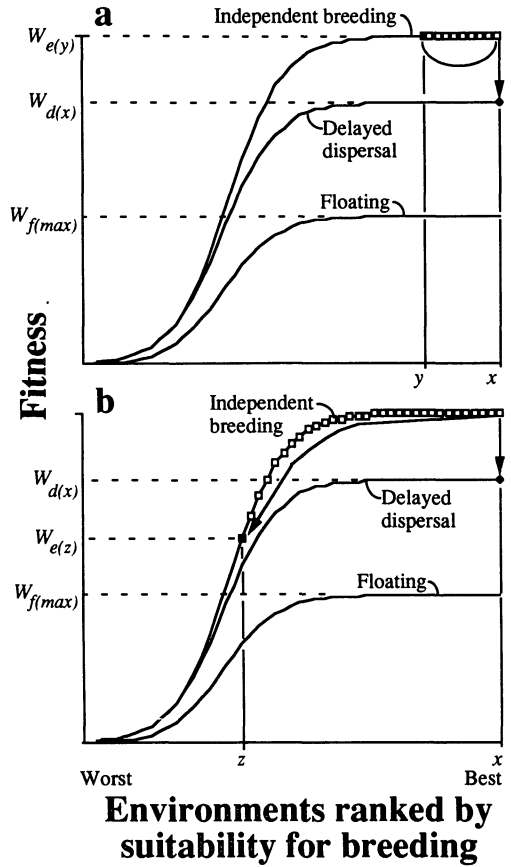**Environments ranked by suitability for breeding**

FIG. 2.   PARAMETERS INFLUENCING THE DELAYED DISPERSAL THRESHOLD MODEL. I. POPULATION DENSITY.

Habitat-fitness gradient curves are graphed as described in Figure 1(b), where extrinsic constraints force delayed dispersal and the fitness of floaters is low. Only territories represented by open square symbols on the "independent breeding" line are occupied, with the highest-quality unoccupied environment represented by a solid square. (a) Low density: An individual born on the best available territory x will be best off dispersing to the best available territory (y) and breeding early, since $W_{e(y)} > W_{d(x)} > W_{f(max)}$. (b) High density: The same individual will be best off delaying dispersal and remaining as a nonbreeder on his or her natal territory x since $W_{d(x)} > W_{e(z)} > W_{f(max)}$.

not "cause" delayed dispersal and cooperative breeding, but is an important factor influencing the probability of these phenomena by affecting the expected fitness of individuals that disperse and breed in the best available territory.

If the intrinsic benefits outweigh the costs [as in Fig. 1(a)], the fitness of individuals that delay dispersal is likely to be greater than for those that disperse and breed regardless of population density, and density consequently has little effect on whether some individuals will delay dispersal (that is, on whether groups will form). However, density will influence group size (e.g., Brown, 1982) since, as density increases, individuals will continue to delay dispersal and group size will increase until the intrinsic benefits to those remaining no longer outweigh the costs. At this point, the decision of whether to delay dispersal or to disperse becomes analogous to the situation in which extrinsic constraints currently provide the proximate factor forcing group living (see Fig. 4 below).

If extrinsic constraints are paramount, dispersal/breeding on a high-quality territory always yields the highest fitness. Thus, in the remaining discussion, we will generally be concerned with the situation in which population density is sufficiently high so as to constrain the ability of offspring to disperse and breed in high-quality territories. Under such conditions, the relative payoff of the options available to offspring depends on the remaining four factors.

2. *Fitness differential between early and delayed dispersal.* Here we include variables that influence the differential between the territory quality gradients representing the delayed dispersal/helping option (curve *d*) and the dispersal/breeding option (curve *e*) (Fig. 1). We discuss four of the most important below. Although we discuss them separately, they are interrelated under most circumstances.

a. *Resource depressibility on territories.* This refers to the degree to which use of a limiting resource by one individual reduces its availability to another (Waser, 1988). If extrinsic constraints promote delayed dispersal, resource depression is one factor determining the magnitude of the drop (within the same territory) from the territory quality gradients of dispersal/breeding to that of delayed dispersal (Fig. 3). The more depressible limiting resources are, the more reproductive success and survivorship are influenced by additional group members, and the more likely it is that parents or other group members might not tolerate delayed dispersal by offspring.
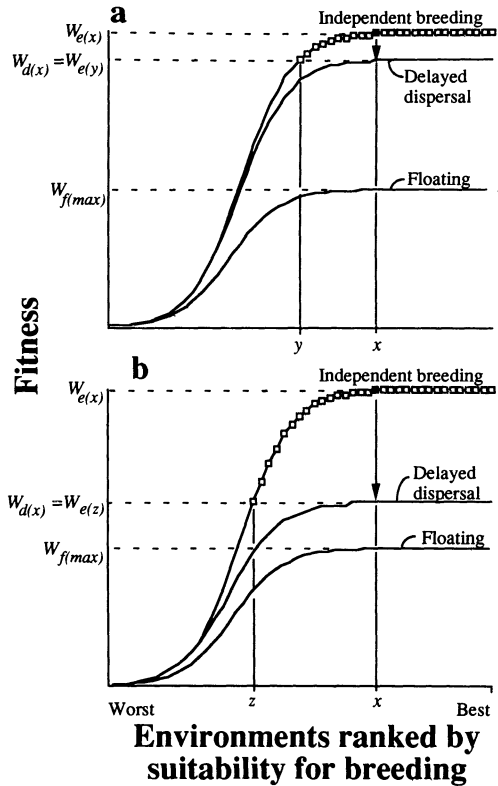

FIG. 3.   PARAMETERS INFLUENCING THE DELAYED DISPERSAL THRESHOLD MODEL. IIA. FITNESS DIFFERENTIAL BETWEEN EARLY AND DELAYED DISPERSAL: EXTRINSIC CONSTRAINTS PARAMOUNT.

(a) If the differential between dispersal/breeding and delayed dispersal is small, the probability that individuals will delay dispersal is relatively high. For example, an individual born on territory *x* must find a vacant territory of quality greater than territory *y* (since $W_{d(x)} = W_{e(y)}$) for early dispersal/breeding to yield higher fitness than delayed dispersal. (b) If the differential between dispersal/breeding and delayed dispersal is great, the probability that individuals will delay dispersal is relatively lower. In this case, an individual born on territory *x* need only find a vacant territory of quality greater than territory *z* (since $W_{d(x)} = W_{e(z)}$) for dispersal/breeding to yield higher fitness than delayed dispersal.

Relatively nondepressible limiting resources [Fig. 3(a)] will reduce the differential between the fitness of individuals that disperse and breed and those that delay dispersal. Under such conditions, delayed dispersal is more

likely to be preferred by offspring and toler-
ated by breeders. Specifically, it will be the
best option for individuals born on territory
x whenever they are unable to obtain a va-
cancy in a territory whose quality is greater
than y [Fig. 3(a)]. In contrast, a high differen-
tial between these options due to high depress-
ibility of limiting resources means that de-
laying dispersal entails a large cost and is less
likely to be preferred by offspring or tolerated
by breeders. In Figure 3(b), only individuals
born on territory x failing to obtain a vacancy
in a territory whose quality is greater than z
should delay dispersal. In both Figures 3(a)
and 3(b), delayed dispersal and independent
breeding are preferred to floating.

Since territory z is of lower quality than y, it
follows that delayed dispersal and cooperative
breeding are more likely when limiting re-
sources are relatively nondepressible [Fig.
3(a)]. The exact consequences of resource de-
pressibility, however, may be difficult to pre-
dict for at least three reasons. First, it is neces-
sary to take into consideration the effects of
resource depression on the fitness of all group
members, since conflicts of interest might
prompt some group members to try and evict
offspring, thereby constraining the latter's
ability to delay dispersal. Second, the degree
of depressibility may be correlated with terri-
tory quality; for example, resource depres-
sion may be less on high quality territories
than on those of moderate to low quality.
Third, individuals may have ways of counter-
acting the effects of resource depressibility.
For example, Florida scrub jays increase their
territory size directly with increasing group
size (Woolfenden and Fitzpatrick, 1984).
Thus, resource depression, which might oth-
erwise be significant as more individuals de-
lay dispersal and group size increases, is les-
sened by the additional resources garnered by
larger groups.

If the intrinsic benefits of delayed dispersal
and group living outweigh the costs, resource
depressibility becomes a major determinant
of optimal group size (e.g., Brown, 1982).
This is shown in Figure 4, the top part of
which [Fig. 4(a)] depicts the situation in
which resources are relatively nondepressible
such that intrinsic benefits continue to out-
weigh the costs up to groups of size six, after
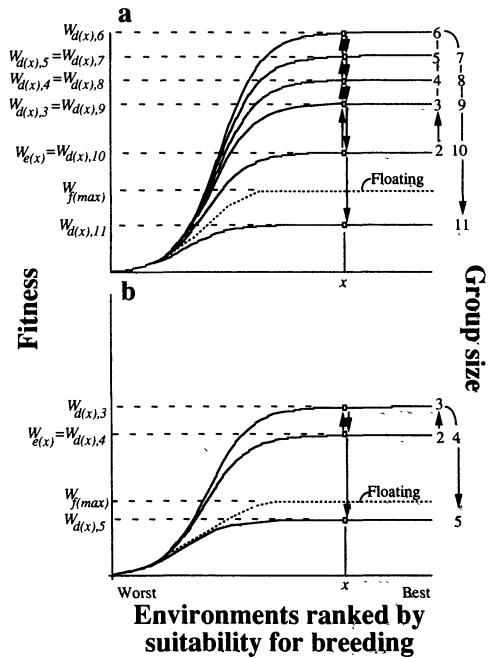which the costs associated with exploitation of

FIG. 4.   PARAMETERS INFLUENCING THE DELAYED
DISPERSAL THRESHOLD MODEL. IIB.
FITNESS DIFFERENTIAL BETWEEN EARLY
AND DELAYED DISPERSAL: INTRINSIC
BENEFITS PARAMOUNT.

This figure graphs parallel habitat-fitness gradi-
ents each of which tracks the fitness of an offspring
depending on the size of the group (represented by
the numeric subscript) while it delays dispersal. (a)
The fitness differential between dispersal/breeding
and delayed dispersal is relatively large and in-
creases to groups of size six. In this case, an indi-
vidual born on territory x continues to gain by
delaying dispersal up to a group with six members.
If the group is larger, the intrinsic benefits of de-
layed dispersal decrease. At groups with 10 mem-
bers, the options of dispersal/breeding indepen-
dently and delayed dispersal yield equivalent
fitness. By assuming that floaters can locate space
in the best available habitat for floating, floating
becomes the preferred option at larger group sizes
unless the individual can find a vacant territory of
quality greater than $W_{f(max)}$ or join a smaller group
with a consequently higher territory quality gradi-
ent. (b) The fitness differential between dispersal/
breeding and delayed dispersal is small and accrues
only up to groups of size three. In this case, an
individual born on territory x gains by delaying
dispersal only if it is the only one to do so; if two
offspring delay simultaneously, their fitnesses are
equivalent to what they could expect by dispersing/
breeding on a territory of comparable quality.
Floating becomes the preferred option at larger
group sizes unless a vacant territory can be ac-
quired of quality greater than $W_{f(max)}$.

the limited resource by additional individuals leads to lower intrinsic benefits. Eventually, when group size is at ten, an additional offspring would be even better off dispersing/floating than delaying dispersal and living in a group of size eleven.

Figure 4(b) presents the condition of high resource depressibility. Delayed dispersal entails intrinsic advantages only up to groups of size three, after which the costs begin to outweigh the benefits and the fitness of individuals delaying dispersal and remaining on their natal territory decreases. In this example, individuals would be better off dispersing/floating than living in groups larger than four. This latter example depicts the situation in which a single offspring achieves highest fitness by delaying dispersal and remaining on the natal territory, but additional offspring do not.

The expected distribution of group sizes under these circumstances is dependent on population density, the fluidity of group membership (Sibly, 1983), and the precise relationships among group size, territory quality and resource depression (Brown, 1982, 1987). Note also that the curves in Figure 4 are all drawn with respect to nonbreeding helpers; analogous curves for breeders or other group members might be different, leading to conflicts of interest among individuals concerning group membership. Thus Figure 4 is not a comprehensive model for optimal group size.

Resource depressibility has long been recognized as a major factor influencing the fitness differential between early and delayed dispersal, and thus of sociality and group living (e.g., Charnov et al., 1976; Altmann et al., 1977; Brown, 1982, 1987; Waser, 1988). Waser (1988) provides a thorough discussion, pointing out four types of relatively nondepressible resources: (1) nonconsumable resources such as dens, sleeping sites, or hibernacula, (2) time-limited resources that disappear whether or not foragers consume them, (3) renewable resources, and (4) essential resources that are superabundant because the population is limited by some other resource. To the extent that a limiting resource falls into one of these categories, resource depressibility is likely to be low, and the probability of delayed dispersal and group living is high.

Several species of cooperative breeders appear to be inordinately dependent on a particular critical resource defining suitable territories; examples include the granaries of acorn woodpeckers (Koenig and Mumme, 1987; Stacey and Ligon, 1987; Koenig and Stacey, 1990), the roosting cavities of green woodhoopoes *Phoeniculus purpureus* (Ligon and Ligon, 1990) and red-cockaded woodpeckers *Picoides borealis* (Walters, 1990; Walters et al., in press), and the burrow systems of several mammals (Walters et al., in press). The relative nondepressibility of such nonconsumable resources is most likely a feature basic to delayed dispersal and cooperative breeding in these species.

b. Group size and composition. The potential importance of group size and composition is shown for the case in which intrinsic benefits are paramount (Fig. 4), but group size can also be important if extrinsic constraints lead to delayed dispersal. For example, the expected indirect fitness benefits to a young Florida scrub jay that delays dispersal are relatively great if no other nonbreeders are present in the group. Reproductive success, however, does not increase in groups larger than three (Woolfenden and Fitzpatrick, 1984). Unless this lack of reproductive enhancement is compensated by increased survivorship of breeders, larger territory size, or some other group-related advantage, additional offspring beyond the first accrue no fitness benefits by delaying dispersal.

Group composition may affect fitness in several ways, the most obvious of which is by the genetic relatedness of individuals delaying dispersal and the group members they may potentially aid (Hamilton, 1964; Williams 1966, Brown, 1974; Hartung, 1977; Emlen and Wrege, 1989). The potential indirect fitness benefits of delaying dispersal and acting as a helper are greatest if helpers provide aid to full siblings, and they decrease as the incidence of polygamy, mate-switching, or extrapair fertilizations increases (e.g., Charnov, 1981; see below). It is thus not surprising that most nonbreeding helpers appear, at least, to be helping their parents raise full siblings (Brown, 1987); future molecular analyses will help to clarify whether this is indeed the case as expected from kin selection theory. In general, greater kinship between potential helpers and subsequent offspring they may

help raise increases the benefits and thus the probability of delayed dispersal [cf. Figs. 3(a) vs. 3(b)]. Besides being an important component of the costs and benefits of delayed dispersal, kinship effects are likely to be especially critical in explaining helping behavior per se (e.g., Emlen and Wrege, 1989).

c. The cost of dispersal. In many cooperatively breeding species, offspring are able to inherit and breed in or next to their natal territory without any dispersal; this occurs commonly in acorn woodpeckers (Koenig and Mumme, 1987), gray-breasted jays (Brown and Brown, 1984), Florida scrub jays (through territorial budding, Woolfenden and Fitzpatrick, 1978, 1984), and at least occasionally in many other species. To the extent that territorial inheritance eliminates what would otherwise be a risky dispersal episode, it lessens the costs of delayed dispersal and thereby decreases the differential between delayed dispersal and dispersal/breeding (assuming that extrinsic constraints provide the proximate impetus for delayed dispersal). The potential importance of territory inheritance and short-distance movements to delayed dispersal has been stressed recently by Stacey and Ligon (1987, 1991) and by S. Zack and B. J. Stutchbury (pers. commun.; Zack, 1990).

A second mechanism by which delaying dispersal could minimize costs might be by permitting dispersal to occur when it will entail relatively little risk. This would occur if, for example, individuals were able to delay dispersal until they were in peak physical condition rather than all dispersing at a set point in time. Equally important, delayed dispersal allows individuals to use the natal territory as a base from which to make forays in search of reproductive vacancies, thereby potentially reducing dispersal costs compared to the alternative of floating (Hooge, 1992). Nonbreeding helper acorn woodpeckers, for example, devote a significant proportion of time to extensive forays of 20 km or more searching for reproductive vacancies, while then regularly returning to their natal territory. One result of these forays is presumably to decrease the potential risks associated with finding and obtaining a reproductive vacancy and thus to raise the "delayed dispersal" gradient [cf. Fig. 3(a) vs. 3(b)]. Long-distance forays

in search of vacancies may be considerably more common in cooperative breeders than usually believed (Hooge, 1992); this is directly contrary to the model proposed by Zack (1990), who suggested that delayed dispersal and cooperative breeding are causally related to short-distance dispersal to adjacent territories of high quality by nonbreeders. More extensive use of radiotelemetry is needed to address this issue.

A third way in which the costs of delayed dispersal may be reduced is by offspring waiting until they can disperse and obtain territories of higher quality than those currently available, thereby ultimately compensating for the loss in fitness due to delayed breeding (S. Zack and B. J. Stutchbury, pers. commun.). This could happen as a consequence of individuals being older and more competitive (e.g., Woolfenden and Fitzpatrick, 1984), having more time to accurately assess territory quality, or having more time to recruit or acquire coalitions of related individuals with which they can fight for reproduction vacancies (Hannon et al., 1985; Hooge, 1992), or exploit as helpers following dispersal (Ligon and Ligon, 1978, 1979). Concurrently, the fitness differential between the dispersal/breeding and delayed dispersal options may increase as the ability of individuals to exploit the resources available on any particular territory increases (see the skill hypothesis, discussed below). If the fitness consequences of delayed dispersal remain constant, this effectively increases the relative advantages of independent breeding and results in progressively lower-quality territories becoming acceptable to a helper as it gets older [cf. Fig. 3(b) vs. 3(a)]. Together, both the increased competitiveness of older individuals and their increased ability to exploit limited resources should result in a preponderance of helpers being young and inexperienced.

High costs associated with dispersal (or, conversely, the potential benefits associated with philopatry) have been suggested to be important to the evolution of delayed dispersal and subsequent helping behavior by numerous authors (e.g., Waser and Jones, 1983; Brown, 1987; Stacey and Ligon, 1987, 1991; Waser, 1988; Zack, 1990; Emlen, 1991). Such costs do not, by themselves, result in delayed dispersal and group living, re-

gardless of how high they may be. Juvenile red grouse *Lagopus scoticus*, for example, suffer extremely high mortality in their first year as a consequence of dispersal and exclusion from high-quality foraging sites by territorial owners (Watson, 1985). This high risk does not result in delayed dispersal by offspring. Two closely related taxa, however, might differ in the degree to which dispersal is risky or in the ways that the risks can be mitigated so as to promote delayed dispersal in one but not the other. All other things being equal, the greater the costs of dispersal, the more probable that delayed dispersal will offer opportunities to mitigate those costs. On the other hand, as in the red grouse example, the magnitude of seasonal resource depression may be so severe that it eliminates the possibility of cooperative breeding by making it impossible to delay dispersal and remain on the natal territory.

By definition, a disperser is a floater until it settles on a breeding territory. Consequently, the cost of dispersal can be viewed as the cost of floating (discussed below) for the time it takes to acquire or settle on a territory, whether it be a few days or several years.

d. Secondary benefits of delayed dispersal and helping. Regardless of the initial impetus to delay dispersal and live in groups, once groups exist individuals can be expected to exploit all potential benefits to group living and helping behavior. If extrinsic constraints provide the proximate impetus for delayed dispersal, the effect of secondary benefits is to raise the delayed dispersal curve. Graphically, this is shown in the difference between Figure 3(b) (few secondary benefits) and Figure 3(a) (high secondary benefits). Otherwise, secondary benefits add to the primary intrinsic benefits to increase optimal group size (e.g., Fig. 4).

Secondary benefits may include both group effects arising from larger group size and alloparental effects arising from helping behavior per se (Koenig and Mumme, 1990). Examples of the former include increased vigilance (e.g., McGowan and Woolfenden, 1989), more efficient exploitation or defense of resources (e.g., Bednarz, 1988), and larger territory size leading to a higher probability of obtaining a territory in the future through territory budding (e.g., Woolfenden and Fitz-patrick, 1978, 1984). Examples of the latter may include increased reproductive success or survivorship of related breeders, either of which would result in greater indirect fitness of individuals delaying dispersal and helping (Brown, 1983, 1985, 1987; Mumme et al., 1989; Koenig and Mumme, 1990). As with the effects of resource depressibility, secondary benefits might differ between high- and low-quality territories. This would be true, for example, if helpers have little effect on high-quality territories containing abundant resources and a relatively large effect on low-quality territories.

The distinction between intrinsic benefits accruing as an immediate consequence of delayed dispersal versus secondary benefits that arise and evolve subsequent to delayed dispersal and group living is a historical one that cannot be made in practice. There are few automatic benefits, however, to group living (Alexander, 1974), and thus most of the intrinsic benefits observed in cooperative breeders are probably derived secondarily. This provides an important cautionary note concerning the significance of such benefits to the evolutionary origin of these phenomena. Although intrinsic benefits may be measurable and significant, it cannot be assumed that they are responsible for a difference in dispersal tendencies between two closely related taxa. This is because intrinsic benefits are, by definition, only available to populations in which delayed dispersal and group living exist, and cannot be observed or measured in closely related, non-group-living populations. Offspring of the non-group-living population might very well accrue similar or identical benefits if they delayed dispersal as well.

This caveat also sets us squarely apart from the views of Stacey and Ligon (1987, 1991), whose benefits of philopatry hypothesis propose that extrinsic constraints to dispersal may be a result rather than a cause of delayed dispersal, which they propose is instead a result of intrinsic benefits to group living. We believe that in a vast majority of cooperative breeders extrinsic constraints are the original cause of delayed dispersal and that most intrinsic benefits resulting from this behavior are secondarily derived.

Despite this caveat, secondary benefits may differ inherently between taxa in ways critical

to the evolution of delayed dispersal. For example, the opportunity to accrue indirect fitness benefits by delayed dispersal and helping may be lower in migratory and nomadic taxa in which relatives are unlikely to remain together compared to nonmigratory taxa in which offspring could remain with their parents and help raise siblings. Similarly, populations subject to high predation pressure might benefit from sentinel behavior in ways that a population living on an island free of predators could not. The importance of some of these factors to delayed dispersal could be tested by appropriate manipulations; for example, if kinship and indirect fitness leading to reduced cost of delayed dispersal is hypothesized to be a critical parameter, one could remove one member of successfully breeding pairs with helpers, thereby opening up the opportunity for replacement by unrelated individuals. Offspring would then have to choose between early dispersal and remaining to raise half-siblings. To the extent that indirect fitness benefits are critical to delayed dispersal, there should be a significant increase in offspring leaving and either floating or attempting independent breeding compared to unmanipulated controls.

One important hypothesis that falls into the category of secondary benefits to delayed dispersal is the skill hypothesis, which proposes that delayed breeding and delayed dispersal allow nonbreeders to acquire experience that increases their lifetime fitness by making them more successful breeders later in life. This idea, first suggested by Skutch (1961), was modeled as a potential explanation for delayed breeding by Brown (1987); it has subsequently been proposed as the cause of delayed dispersal and cooperative breeding in white-winged choughs and in a variety of other species by Heinsohn and his colleagues (Heinsohn et al., 1990; Heinsohn, 1991).

There are at least two difficulties with this hypothesis as an explanation for delayed dispersal and cooperative breeding. First, although young individuals may lack the skills necessary to breed successfully, there is no a priori reason to believe that the most efficient way to acquire such skills is by delayed dispersal and helping. They might be acquired equally efficiently by floating or even by attempting to breed independently, albeit with

small probability of success, as occurs in the noncooperative western scrub jay (Carmen, in press). Second, the skill hypothesis proposes a mechanism that potentially yields intrinsic benefits to delayed dispersal. Like other aspects of delayed maturity, however, if the acquisition of breeding skills is purely a matter of slow or delayed development, then it is a secondary effect, not a cause, of delayed dispersal (Koenig and Pitelka, 1981).

This distinction has misled some authors to confuse the ecological circumstances causing the current adaptive utility of delayed dispersal and the mechanism promoting this behavior. For example, consider the white-winged chough in which young require considerable time to acquire the skills necessary for independent reproduction. Heinsohn et al. (1988, 1990; Heinsohn, 1991) have argued that this constitutes a significant intrinsic advantage to delayed dispersal and cooperative breeding to the extent that these behaviors are obligatory in the population. Delayed dispersal in white-winged choughs, however, may have initially been selected due to extrinsic constraints. Once offspring progressively lost the opportunity to disperse early and breed independently, it is likely that selection favored individuals that devoted their limited time and energy to behaviors of more immediate fitness value than acquiring breeding skills early, which they will only get to use much later in life. This would then set up the potential for coevolution between delayed dispersal and the behavioral skills necessary for breeding: as early dispersal/breeding became more and more constrained, acquisition of the skills needed for early breeding would become more and more delayed (Creel and Creel, 1991).

A second example mixing mechanism and current function is provided by Richner (1990), who argued that the phenotypic constraint of small body size has restricted the dispersal options of some young male carrion crows (*Corvus corone*), and has led to delayed dispersal and helping. As support for this hypothesis, he cites the observation that the three male helpers he observed were at or below the size limit of territorial males in the population. This argument, however, confuses the mechanism by which an ecological constraint is imposed with the constraint it-

self: if there were no constraint on independent reproduction due to limited breeding opportunities in high-quality habitat, even the smallest males could disperse and breed on their own. Once breeding opportunities are restricted, it is not surprising that the largest and presumably strongest individuals should occupy territories, forcing smaller individuals to choose alternative dispersal options.

There is, however, one situation where we can envision that the skill hypothesis might be important to delayed dispersal and helping behavior. If offspring learn breeding skills specifically by observing other group members, then delayed dispersal would confer proximate intrinsic benefits that might render delayed dispersal and group living essential to the fitness of individuals, rather than simply a consequence of the extrinsic factors originally constraining independent reproduction. This in turn could significantly improve the cost-benefit ratio of delayed dispersal/helping compared to either dispersal/breeding or dispersal/floating. Thus, assessment of the current role of the skill hypothesis to the evolution of cooperative breeding is dependent, in part, on detailed observations of the ontogeny of breeding skills. Such data have yet to be acquired for any species, although the data provided by Heinsohn (1991) on the white-winged chough are a promising start in this direction.

3. Fitness of floaters. As discussed above, the fitness of floaters is determined primarily by a combination of their survivorship and their effectiveness in finding mates and high-quality breeding territories. Although not yet demonstrated, it is also possible that floaters in some species may increase their fitness by obtaining EPCs or, in the case of females, by intraspecific brood parasitism. Factors influencing the fitness of floaters have often been ignored by prior treatments of the evolution of delayed dispersal/helping, although recent work by Carmen (in press) and reviews by P. Arcese (pers. commun.) and S. Zack and B. J. Stutchbury (pers. commun.) are beginning to change this.

Figure 5 focuses on the potential importance of the fitness of floaters to whether or not individuals in a population will breed cooperatively. In Figure 5(a), two territory quality gradients for floaters are drawn. In the
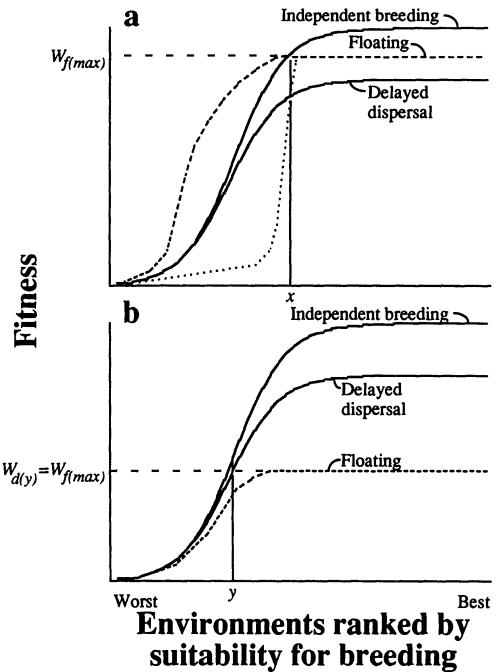

FIG. 5. PARAMETERS INFLUENCING THE DELAYED DISPERSAL THRESHOLD MODEL. III. FITNESS OF FLOATERS.

Floaters may have either high or low fitness depending on the quality of habitat available to them and their success at finding and filling breeding vacancies in high-quality habitat. (a) Floater fitness in the best habitats is high, while floater fitness in habitats of poor quality for breeding is high (dashed line) or low (dotted line). In either case, an individual may be better off floating than delaying dispersal if floaters can locate space in high-quality floater habitats. If floater fitness in habitat poor for breeding is high, floating may still be better than delayed dispersal; this is unlikely if floater fitness in habitats that are poor for breeding is low. (b) If floater fitness even in the best habitats is low, only those few individuals born on territories of lower quality than y would be better off floating than delaying dispersal and remaining as a nonbreeder on their natal territory, even if floaters have some access to high-quality habitats. Individuals born on higher-quality territories are better off delaying dispersal than floating.

first, represented by the dashed line, floaters have high fitness, even in some habitats of poor quality for breeding, presumably because they survive well and can later locate vacant territories of high quality efficiently,

even though the area lacks some resource critical for successful breeding. Under these conditions, floaters could still have relatively high fitness even though they meet considerable aggression from breeders in high-quality (breeding) territories. In the second, represented by the dotted line, floaters have high fitness only in the territories of high quality for breeding. This is the more likely situation if critical resources are similar for breeders and floaters.

The probability of floating under the conditions depicted by Figure 5(a) is largely dependent on whether or not floaters are excluded from high-quality habitats. If they are not, then floating is preferable to delayed dispersal for all individuals, even those born on the best territories, since $W_{f(max)} > W_d$ for all environments. Examples include California scrub jays (Carmen, in press) and the rufous-collared sparrow (Smith, 1978). If floaters are discouraged from occupying high-quality breeding habitat, floating is still preferable to delayed dispersal if the fitness of floaters is high in a habitat that is suboptimal for breeding (the dashed line). This may correspond to the situation found, for example, in Santa Cruz Island scrub jays (Atwood, 1980) and common crows (Caffrey, 1991), where floaters appear to survive well in peripheral areas not suitable for breeding.

If the fitness of floaters is low in habitat suboptimal for breeding [the dotted line in Fig. 5 (a)], then delayed dispersal is likely to be preferable assuming floaters are excluded from high-quality habitats. This effectively puts floaters in the situation shown in Figure 5(b), where the fitness of individuals that disperse and float is poor even in the highest-quality habitats. Under the conditions shown, only individuals born on territories whose quality is worse than territory y could profit by floating rather than remaining as non-breeders, since $W_{f(max)} < W_d$ for all territories whose quality is greater than territory y. Thus, delayed dispersal/helping is more likely if the fitness of individuals that disperse and float is lower, as in Figure 5(b). Note, however, that in both cases graphed in Figure 5, individuals are best off dispersing/breeding independently if they are able to acquire a high-quality territory.

Just as for individuals dispersing to vacant territories, the quality of habitat that is acceptable to a floater is dependent on several factors. For example, progressively lower-quality territories should become acceptable to floaters with time if their survivorship (and hence fitness) is age dependent. Given the static situation depicted in Figure 5, floaters with high fitness [Fig. 5(a)] should choose to disperse and breed only if they can fill a vacancy in a territory of quality greater than x, whereas those with low fitness [Fig. 5(b)] should be willing to accept any territory of quality greater than y.

Floaters are difficult to observe and have rarely been documented in cooperative breeders, much less has their fitness been accurately assessed (but see Walters et al., 1992). However, if floaters are found in a noncooperatively breeding taxon closely related to one that exhibits cooperative breeding, the factors influencing floater fitness are likely to be important to understanding their differing social behaviors. An example is the scrub jay complex, discussed in detail below.

4. Distribution of territory quality. We divide our discussion of this issue into three parts, discussing first the marginal habitat hypothesis, then alternative models for the importance of the distribution of territory quality, and finally how one factor, sex ratio bias, can act via its effect on the distribution of territory quality to influence the probability of delayed dispersal.

a. The marginal habitat hypothesis (MHH). This hypothesis proposes that there are relatively many optimal territories of high quality and few marginal territories of intermediate or low quality, leading to a steep territory quality gradient [Fig. 6(a); Koenig and Pitelka, 1981]. Under these conditions, population density (habitat saturation) is likely to be high, since survivorship and reproductive success are by definition very good on high-quality territories. Many offspring, virtually all of which are (again by definition) born on high-quality territories, are unlikely to disperse and breed independently, since all high-quality territories are usually filled, and there are few acceptable territories of marginal quality.

Consider an individual born on territory x [Fig. 6(a)]. The best option is to disperse and breed as long as a vacancy can be obtained in
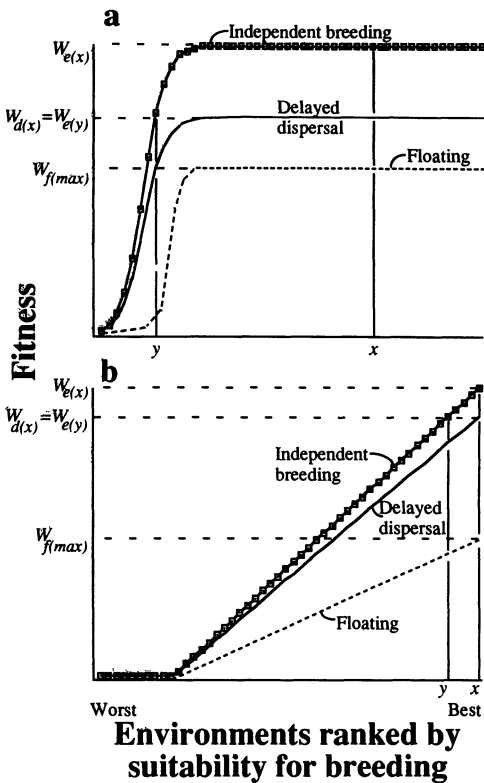
FIG. 6. PARAMETERS INFLUENCING THE DELAYED DISPERSAL THRESHOLD MODEL. IV. DISTRIBUTION OF TERRITORY QUALITY.

(a) Conditions characterizing delayed dispersal according to the marginal habitat hypothesis (Koenig and Pitelka, 1981). This model postulates a high proportion of high-quality (optimal) compared to marginal territories. Under these conditions, delayed dispersal will be the best option for offspring as long as population density is high, whether the fitness differential between dispersal/breeding and delayed dispersal is large or small. (b) Conditions promoting delayed dispersal according to the variance hypothesis (Stacey and Ligon, 1987, 1991; see text). This model postulates wide variation in territory quality and can lead to delayed dispersal even under conditions of low density as long as the fitness differential between dispersal/breeding and delayed dispersal is small.

a territory of quality greater than y. These, however, are nearly all high-quality territories and are unlikely to offer more than an occasional vacancy, for which competition from other offspring will be intense. Thus delayed dispersal will be the best option available to a large proportion of offspring, even when the fitness differential between delayed dispersal and dispersal/breeding is relatively large [Fig. 6(a)]. Floating is also likely to be an inferior option because the MHH suggests that suitable habitat is relatively homogeneous and generally fully occupied. Any unoccupied habitat is likely to be of poor quality, and if floaters are restricted to such a habitat, their fitness is likely to be low. Other distributions of habitat quality are less likely to constrain floating in this way.

Unfortunately, the determination of territory quality is difficult, and thus testing the MHH or any other model for the distribution of territory quality is not easy. Most attempts to do so are flawed by defining territory quality in terms of the reproductive success or survivorship of the occupants (e.g., Stacey and Ligon, 1991). Besides being circular, this procedure is likely to yield misleading results as a consequence of differences in population density, variance in individual performance, and random environmental factors. For example, some areas within the periodically burned scrub favored by Florida scrub jays produce vastly greater numbers of offspring than others, but jays do not compete more vigorously for those areas. This suggests that observed productivity differences are due to differences among lineages rather than differences in habitat quality (Fitzpatrick et al., 1988).

There are at least two additional problems in determining the distribution of territory quality. First, the quality of individual territories may change from year to year, and second, study areas are unlikely to include a representative range of territories to which individuals might potentially disperse, thereby yielding a biased estimate of the distribution of territory qualities. Given these difficulties, it is not surprising that tests of the MHH have produced conflicting results (Koenig and Pitelka, 1981; Emlen, 1991; Stacey and Ligon, 1991; McCallum et al., in press).

b. Alternative models. Conditions favoring delayed dispersal are also possible with other distributions of territory quality besides the steep gradient postulated by the MHH. For example, consider the territory quality gradient shown in Figure 6(b), in which there is a relatively wide range of territory qualities

leading to relatively great variance in the quality of occupied territories. Under these conditions, population density (habitat saturation) is likely to be low, since proportionately few territories are of high quality.

This, however, does not preclude delayed dispersal being the preferred option for at least some offspring. Consider an individual born on the best territory, x, in Figure 6(b). Assuming that the cost to delayed dispersal is small and the fitness of floaters is low, delayed dispersal is the best option as long as no vacancy can be obtained in territories of quality $\geq y$. Since these are all still high-quality territories, this might be true and thus delayed dispersal will probably be the best option for this individual.

As part of their benefits of philopatry model, Stacey and Ligon (1987, 1991; see also Waser, 1988) propose that there is high variance in territory quality among cooperative breeders, and that the quality of occupied territories is relatively uniform among noncooperative breeders; this is contrary to the prediction of the MHH. In order to disinguish this aspect of their model from Stacey and Ligon's (1987, 1991) focus on the benefits of group living, we will call it the "variance hypothesis" (VH), and propose Figure 6(b) as a graphical representation of the distribution of territory quality it predicts should result in delayed dispersal and cooperative breeding.

An important contribution of the VH is that it highlights the importance of taking territory quality into account when comparing the options separately available to each individual in the population (S. Zack and B. J. Stutchbury, pers. commun.). In other words, early dispersal/breeding may be the best option available to one individual, while delayed dispersal/helping may be better for another, depending on the quality of the territory in which they reside. We would go even further and suggest that individual quality may also be an important factor for determining the preferred option for an individual. For example, individuals may differ in their competitiveness for reproductive vacancies; those that are most competitive might be best off dispersing early while those that are not might best delay dispersal until they are older. Thus, a complete understanding of the costs and benefits of each option available to offspring

will require not only knowledge of territory quality, but knowledge of individual quality as well.

If population density is low, delayed dispersal can be preferable to dispersal/breeding for some offspring under conditions specified by the VH, but not the MHH. If population density is high, both predict delayed dispersal among at least some offspring. Thus, in terms of the choice between delayed dispersal/helping and dispersal/breeding, the issue is not whether one model or the other predicts the occurrence of delayed dispersal and cooperative breeding, but rather which model corresponds more closely to the conditions leading to these phenomena in a specific population. The VH is potentially appropriate when relative density and the fitness differential between dispersal/breeding and delayed dispersal are low, while the MHH is potentially applicable when relative density is high, regardless of the fitness differential between dispersal/breeding and delayed dispersal.

c. *Sex ratio bias.* This factor can influence the distribution of territory quality in a population to the extent that a given territory contains (or is capable of attracting) a breeder of the opposite sex. Consider a male born on territory x with the territory quality gradients for dispersal/breeding and for delayed dispersal shown in Figure 7(a). He should disperse and breed if he can find a territory of quality greater than y. If the sex ratio is male biased, however, there will be some fraction of lower-quality territories that will not attract females. If the fitness of lone males on a territory is low and there are only enough females to provide mates for males living on territories of higher quality than z, then in effect the habitat-fitness gradient for individuals dispersing/breeding (and for hypothetical offspring delaying dispersal) falls precipitously in territories of quality less than z [Fig. 7(b)]. In contrast to the original situation, there are now significantly fewer territories acceptable for independent reproduction, and the probability that delayed dispersal will be chosen by some individuals is correspondingly increased.

Thus the sex ratio, to the extent that it influences the availability of mates, is an important factor potentially influencing the expected fitness payoff of delayed dispersal compared

a

Independent breeding

$W_{e(x)}$

$W_{e(y)} = W_{d(x)}$

Delayed dispersal

$W_{f(max)}$

Floating

Fitness

y x

b

Independent breeding

$W_{e(x)}$

$W_{d(x)}$

Delayed dispersal

$W_{f(max)}$

$W_{e(y)}$

Floating

Worst y z x Best

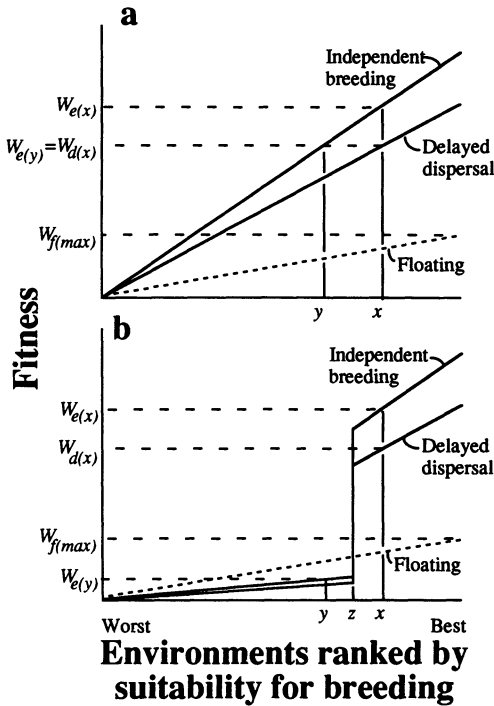**Environments ranked by suitability for breeding**

FIG. 7.   THE EFFECT OF SEX RATIO ON DELAYED DISPERSAL.

(a) Even sex ratio: An individual born on territory x need only find a territory of quality greater than y for dispersal/breeding to be the preferred option. (b) A biased sex ratio: Only enough individuals of the rarer sex to occupy territories of quality greater than or equal to z are assumed to exist. The fitness of individuals that occupy territories without a member of the opposite sex is presumably low, causing a severe steepening of the habitat-fitness gradients for dispersal/breeding and delayed dispersal. Under these conditions, an offspring born on territory x that does not find a vacancy with a mate on a territory of quality greater than or equal to z is best off floating, assuming (in the example shown here) that floaters can occupy space in the best available habitats for floating.

to dispersal/breeding. Like the other factors we consider here, however, a biased sex ratio is not a general explanation of delayed dispersal in cooperative breeders, as evidenced by both the existence of nonbreeders of both sexes in many cooperative breeders (e.g., Florida scrub jays, Woolfenden and Fitzpatrick, 1984; acorn woodpeckers in California, Koenig and Mumme, 1987) and the existence

of a biased sex ratio in many species of noncooperative breeders (Koenig and Pitelka, 1981).

5. Environmental variability. Thus far we have assumed that the relative quality of different territories remains stable over time, leading to fitness gradient curves that are predictable from year to year. This is always going to be an oversimplification.

On a local scale, and more so for some habitats and foraging patterns than others, territory × year interactions due to spatiotemporal variability in resource availability, predator pressure, or sex ratio among territories may be so great that the ranking of territory quality may vary considerably from year to year (Waser, 1988). Regardless of what the habitat-fitness gradients look like during a single season, low predictability in the ranking of relative territory quality over time will reduce the long-term variance in overall territory quality (Stacey and Ligon, 1991). In the extreme case, many individuals would be forced to abandon their previously suitable territories each year and start over elsewhere. This happens to acorn woodpeckers in years when the acorn crop fails (Hannon et al., 1987). These territories would be settled according to dominance status, priority, or whatever factors make some individuals more competitive than others.

Waser (1988), Powell (1989), Zack (1990), and Stacey and Ligon (1991) all suggest that increased spatiotemporal variation will lower the probability of delayed dispersal and cooperative breeding by decreasing the potential fitness payoff of this option compared to dispersal/breeding; thus, extended natal philopatry is likely to be found in species in which territory quality is highly predictable over time. In addition, we propose two reasons for why the option of floating might be relatively better under conditions of high spatiotemporal variation. First, the maximum fitness of an individual that either delays dispersal or disperses and breeds is lower, thereby making these options less desirable. Concurrently, the unpredictability of relative territory quality from year to year makes it more likely that floaters, because of their mobility, will be able to gain access to high-quality areas where resources are more abundant and possibly even suitable for breeding; this will increase the fitness of the floating option. All of these fac-

tors would tend to decrease the likelihood of delayed dispersal compared to alternative dispersal options as spatiotemporal environmental variation increases.

Second, fitness × year interactions due to annual differences influence the absolute quality, but not the relative ranking, of individual territories. Annual differences in reproductive success and survivorship within a population would result. The fact that in good years, previously poor territories may become of sufficiently high quality to support breeding may be equally important. Individuals taking advantage of such temporarily outstanding conditions may have previously been either nonbreeding helpers, floaters, or breeders on lower-quality territories. Variation differentially influencing territory quality (but not enough to alter their relative ranking), might also alter the shape of the habitat-fitness gradient curves and thereby influence the probability of delayed dispersal as discussed in prior sections.

The primary effect of such annual variation in conditions is to temporarily increase (or decrease) the relative density of the population, both by altering the average absolute fitness of individuals in the population, thereby resulting in larger (or smaller) population size, and by increasing (or decreasing) the average absolute quality of territories, and thus directly altering the amount of occupiable space. These factors directly determine the degree of habitat saturation (defined as relative density) and thus the likelihood of delayed dispersal, as discussed earlier. In particular, relative density is likely to vary considerably from year to year, leading to wide variation in the observed proportion of offspring choosing the various dispersal options depending on the current environmental conditions relative to population density.

A Categorization of Factors Influencing Delayed Dispersal and a Comparison with Models for Territorial Polygyny

A flowchart summarizing the factors discussed above as potentially influencing delayed dispersal is presented in Figure 8. All modern hypotheses for the evolution of delayed dispersal in cooperative breeders invoke ecological constraints in the sense proposed by Emlen (1982a). This includes cases in which

intrinsic benefits to delayed dispersal outweigh the costs [Fig. 1(a)], as well as those in which extrinsic factors currently exercise proximate constraint on dispersal [Fig. 1(b)]. Both of these conditions postulate that delayed dispersal is a consequence of a restricted ability to breed independently (Emlen, 1982a; Koenig and Mumme, 1987: 383). In the case of extrinsic constraints, the ecological constraint is typically lack of high-quality breeding space, while in the case of intrinsic benefits, the ecological constraint acts on the ability of pairs without helpers to acquire sufficient resources (other than space) to breed successfully.

If intrinsic benefits are paramount, the five parameters discussed above and numbered in Figure 8 then interact to determine optimal group size. If extrinsic constraints force delayed dispersal, these same five factors interact to determine the probability of delayed dispersal for any particular individual. For the five parameters discussed above, some important additional subcategories discussed earlier are also included.

These five parameters are not mutually exclusive. Indeed, they are best thought of as axes in five-dimensional space, certain sections of which specify conditions favoring delayed dispersal and cooperative breeding while others favor delayed breeding with floating and still others dispersal with early breeding. No one factor by itself causes delayed dispersal in general, but a difference in the dispersal patterns observed between two species or populations may be attributable to a small subset or even a single factor. The challenge to future workers in this field is to identify these factors in specific cases.

In Table 1 we go a step further and summarize the major ways in which the ecological, demographic and environmental factors discussed above are likely to influence the choice among the three dispersal options. Given the number of these variables, combined with the likelihood that many of them interact in complex ways, it is not surprising that the evolution of delayed dispersal and cooperative breeding has proven to be an uncommonly interesting phenomenon.

In Table 2 we offer a comparison of different forms of the delayed-dispersal threshold model with the classification of models for the
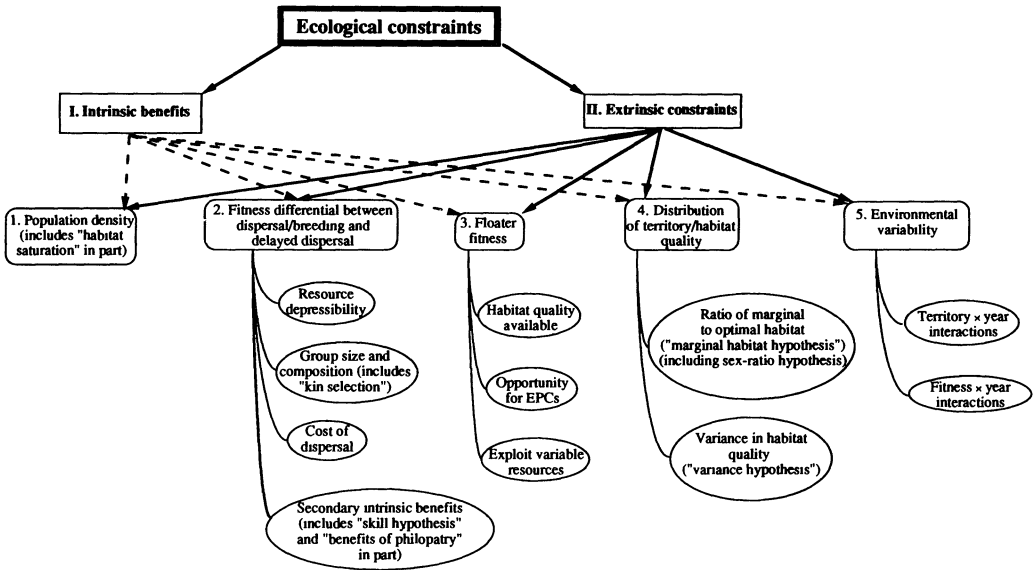
Fig. 8. A Flowchart Summarizing Factors Influencing Delayed Dispersal and the
      Occurrence of Cooperation.

All current hypotheses invoke ecological constraints. These constraints consist of varying combinations of intrinsic benefits and extrinsic constraints on the ability of offspring to obtain high-quality breeding opportunities. If intrinsic benefits are paramount, delayed dispersal will be a preferred option for at least some offspring; if extrinsic constraints are paramount, some offspring may or may not be forced to make the best of a bad job and delay dispersal and help. In either case, the five numbered parameters will be important in determining the extent of delayed dispersal and consequent group size. Important variables determining the influence of these five parameters on the best available dispersal option for offspring are also listed.

TABLE 1

A categorization of factors influencing the relative fitness of dispersal options available to offspring

	Dispersal and independent breeding	Delayed dispersal	Dispersal and floating
I. Intrinsic benefits	low	high	low
II. Extrinsic constraints	low	high	high
1. Population density	low	high	high
2. Fitness differentials			
Resource depressibility	high	low	high
Group size	large	small	large
Group composition	nonrelatives	relatives	nonrelatives
Cost of dispersal	low	high	low
Secondary intrinsic benefits	low	high	low
3. Floater fitness			
Quality of habitat available to floaters	poor	poor	good
Ability of floaters to exploit variable resources	poor	poor	good
4. Distribution of territory quality			
Ratio of optimal to marginal habitat (marginal habitat hypothesis)	low	high	high
Variance in territory quality (variance hypothesis)	low	high	high
Sex ratio	even	biased	biased
5. Environmental variability	high	low	high

Qualitative values specify the relative conditions favoring a particular dispersal option.

TABLE 2

*A comparison of the delayed dispersal threshold model with Searcy and Yasukawa's
(1989) classification of models for the occurrence of territorial polygyny*

Territorial polygyny	Delayed dispersal
I. Male-coercion model	(Parents force offspring to delay dispersal)
II. Female-choice models	Offspring choose to delay dispersal
A. No-cost models	Intrinsic benefits important
1. Benefit models	Intrinsic benefits paramount *or* secondary benefits compensate for costs
2. No-benefit models	Secondary benefits balance costs
B. Cost models	Extrinsic constraints paramount
1. Skewed-sex-ratio model	Shortage of potential mates limits breeding opportunities
2. Balanced-sex-ratio models	No shortage of potential mates
a. Compensation model	Offspring delaying dispersal are compensated by remaining on a territory of high quality
b. No-compensation models	Offspring are not compensated for the cost of delayed dispersal
i. Search-cost model	Offspring delay dispersal because searching for unoccupied territory of suitable quality is costly
ii. Deception model	(No parallel)
iii. Maladapted-female model	Offspring choose delayed dispersal even though superior alternatives are available to them

Scenarios in parentheses are not known to occur and are listed for comparative purposes only.

occurrence of territorial polygyny presented by Searcy and Yasukawa (1989). Given that parents are unlikely to be able to force offspring to delay dispersal, all models for delayed dispersal are analogous to female-choice models for polygyny. As in the polygyny threshold model, factors leading to delayed dispersal can then be divided into "no-cost" and "cost" versions, corresponding to whether intrinsic benefits or extrinsic constraints are paramount. [These alternatives are also analogous to the "cooperative female choice" and "competitive female choice" models for polygyny discussed by Altmann et al. (1977).] Similarly, different versions of cost models involve uneven or balanced sex ratios. The majority of our discussion above, however, focuses on the analog of the "compensation" model (Table 2, IIB2a) in which females are compensated for the cost of polygyny by acquiring a male with a high-quality territory. For delayed dispersal, this corresponds to the situation in which offspring are compensated for the cost of delayed dispersal by remaining on a high-quality (usually their natal) territory, where they may have high survivorship, be able to search for vacancies, acquire secondary benefits, and achieve indirect fitness benefits by helping to raise nondescendant kin.

We have not directly discussed analogs of the "no-compensation" models (IIB2b) listed in Table 2. The most likely scenario in this category is the "search-cost" model analog, which proposes that offspring may delay dispersal because finding vacancies in high-quality territories is costly, even though they exist. This effectively augments the cost of dispersal, decreasing the relative benefits of the dispersal/breeding option and thus increasing the probability of delayed dispersal, as discussed in earlier sections.

UNANSWERED QUESTIONS

Here we briefly discuss some of the more perplexing problems and unanswered questions concerning the evolution of cooperative breeding.

The relative significance of floating. As discussed earlier, most prior theories for the evolution of cooperative breeding are based predominately on the alternatives of dispersal/breeding versus delayed dispersal/helping. This contrast may explain differences in group size in cooperative breeders and, in specific populations, delayed dispersal, but fails to consider, much less explain, dispersal/floating in noncooperative populations.

The problem of floaters is highlighted by the recent study by Carmen (in press) comparing noncooperative and cooperative populations of *Aphelocoma* jays. His study population in central coastal California is representative of noncooperative scrub jay populations in western North America. By drawing on the extensive data available for the cooperative Florida race of this species (e.g., Woolfenden and Fitzpatrick, 1984) and the congeneric gray-breasted jay (e.g., Brown and Brown, 1990), Carmen found that demographic differences among these forms are slight, with nearly identical levels of breeder survivorship and reproductive success. Indeed, the demographic patterns suggest that space competition in noncooperative populations, such as the Santa Cruz Island scrub jay (Atwood et al., 1990), may equal or exceed that found in the cooperative populations. It follows that differences in the degree of space competition per se cannot be the cause of the differences in dispersal options chosen by offspring in this complex.

As mentioned earlier, some cooperative breeders are dependent on a localized, limited and essential resource that apparently constrains both early independent breeding and floating. No such specific habitat feature is implicated in leading to delayed dispersal of either Florida scrub jays or gray-breasted jays. Although constraints on breeding may still be evident in these species, it is more difficult to explain why delayed dispersal is favored over floating.

In Florida, young scrub jays wander freely, but in autumn increased aggression from other groups restricts nonbreeders to either their natal territories or to tracts of unburned scrub. Woolfenden and Fitzpatrick (1984) argue convincingly that unburned areas, which are generally unsuitable for breeding except at very low densities (see Woolfenden and Fitzpatrick, 1991), are also unsuitable for floating; hence both breeders and nonbreeders are restricted to a narrow range of acceptable habitat. Woolfenden and Fitzpatrick (1984) suggested that little marginal habitat exists in Florida compared to the western United States, and this is consistent with the importance of the distribution of territory quality as proposed by the marginal habitat hypothesis (see above).

Additional evidence comes from Atwood (1980), who found that nonbreeding Santa Cruz Island (California) scrub jays disperse and form loosely organized flocks that exploit a wide range of habitats largely unsuitable for breeding. In contrast, on the California mainland, nonbreeders are tolerated on both their natal and other established territories except during the height of the breeding season, and occur in loose flocks in habitats containing the most abundant resources (Carmen, in press). As in rufous-collared sparrows (Smith, 1978), floaters on the mainland use habitat occupied by breeders, and the presence or absence of unoccupied marginal habitat may not be the critical factor limiting dispersal/floating. These studies suggest that constraints on or benefits of early dispersal/floating, rather than constraints on independent breeding, is the critical factor distinguishing cooperatively from noncooperatively breeding jays.

If this is true, what are the underlying ecological factors that contribute to different levels of floater fitness? An important difference may be the seasonal abundance and distribution of acorns. Each autumn, individual scrub jays in Florida (DeGange et al., 1989) and in California (Carmen, in press) cache 5000 to 8000 acorns for use during the winter and early spring. In California, poor acorn years result in significantly higher mortality, reproductive failure, and territory abandonment (Carmen, in press). Comparable data are not available from Florida, because acorn production is regular in both space and time; over an eleven-year period, for example, no acorn crop failures were detected (DeGange et al., 1989). Assuming that scrub jays are as dependent on acorns in Florida as in California, the very low occurrence of acorn crop failure would prevent local population crashes. Moreover, in Florida, the low but even density distribution of acorns contributes to a situation where territory defense is economical, intruder pressure is slight, and floaters probably do not have the option of living in occupied areas.

But why is floating in unoccupied areas not a viable option? Woolfenden and Fitzpatrick (1984) suggest that high predation rates in unburned scrub and other marginal habitats outside of occupied areas are responsible, but differences in acorn production could also be important. If acorn production declines with

age of sprouts, as found for scrub oak in New Jersey (Wolgast and Stout, 1977), this would provide at least one reason why periodically burned scrub is so highly prized by Florida scrub jays and why floating in denser, unburned scrub is not favored.

In contrast, acorn production by the large and patchily distributed oaks of several species in California is highly variable locally within and among years with periodic crop failures four to six years apart (Hannon et al., 1987), depending in part on the number of oak species in an area (Carmen et al., 1987). Individual large oaks may produce hundreds of thousands of acorns in good years. Early dispersal may be favored as floaters aggregate in areas of high acorn abundance, and the tolerance of floaters by breeders allows them access to the best habitats. Floaters are also free to move regionally and search out breeding areas where populations have declined due to crop failures (Carmen, in press). Currently, little is known about acorn production patterns in either gray-breasted jay or Santa Cruz Island scrub jay habitats, or the degree to which these jays depend on acorns. Such data would be of particular interest in the gray-breasted jay, as no obvious habitat or vegetation features separate high-quality habitats from poor ones in this plural-breeding species (Brown and Brown, 1985; Edwards, 1986). Indeed, Brown (1986: 781) states that "although individuals are free to disperse and explore to find suitable areas elsewhere, they rarely do."

Unfortunately, it is not possible to directly test for differences in floater fitness because floaters are rare in Florida and range widely in California. Clearly, though, the phenomenon of floaters, their significance as a dispersal option, and their variable occurrence as a demographic subclass among cooperatively breeding species calls for more extensive comparative study.

Co-occurrence of delayed dispersal and early dispersal/floating. Four species in which these dispersal strategies are known to regularly coexist are the Australian magpie (Carrick, 1972; Veltman, 1989), purple gallinule (Hunter, 1987), common crow (Caffrey, 1991), and red-cockaded woodpecker (Walters et al., 1992). The Australian magpie is particularly notable because of the wide range in strategies

apparently employed by individuals attempting to obtain high-quality breeding opportunities. Otherwise, these dispersal options rarely appear to overlap within a single population, or even (with the notable exception of the scrub jay) within the geographic range of a single species. This is surprising given the wide range of ecological settings inhabited by some cooperatively breeding species (e.g., acorn woodpeckers; Koenig and Stacey, 1990) and by some genera, such as *Pomatostomus* in Australia, all of whose species are cooperative breeders (Edwards and Naeem, in press).

Conditions leading to delayed dispersal/helping versus cooperative polygamy. In addition to the simplest form of cooperative breeding, in which offspring delay dispersal and subsequently act as nonbreeding helpers on their natal territory, cooperative breeding also includes cooperative polygamy (Faaborg and Patterson, 1981) and plural breeding (Brown, 1987), in which two or more individuals of the same sex share breeding status within a social unit. Plural breeding usually involves multiple pairs of breeders within a social unit, while cooperative polygamy may involve cobreeding males that share one or more females and joint-nesting females that share one or more males in virtually any combination (see Brown, 1987, Table 2.2).

On the basis of their differing models, Stacey (1982) predicted that mate-sharing should occur when there are significant intrinsic benefits to all individuals, while Vehrencamp (1983) predicted that societies in which individuals share mates equally should occur when intrinsic benefits are weak or absent, and thus extrinsic constraints lead to this phenomenon. Empirical studies have similarly come to diverse conclusions. Stacey (1979b, 1982) found that intrinsic benefits leading to increased reproductive success were important to mate-sharing by male acorn woodpeckers in New Mexico, while in California, both extrinsic constraints and intrinsic benefits appear to be important to mate-sharing males and joint-nesting females (Koenig and Mumme, 1987; Mumme et al., 1988). Koford et al. (1986) found good evidence that extrinsic constraints, possibly in the form of nest sites, are important to the evolution of plural breeding in groove-billed anis, but also

found a role for intrinsic benefits of group living. Rowley et al. (1989) concluded that plural breeding in the splendid fairy-wren (*Malurus splendens*) was primarily a function of extrinsic constraints in the form of increased population density. Finally, work by Davies and his colleagues (Davies and Houston, 1986; Burke et al., 1989; Davies 1990) on dunnocks (*Prunella modularis*) demonstrates that intrinsic benefits modulated by conflicts of interest between males and females are important in maintaining their variable mating system. Thus current empirical data provide support for almost any combination of intrinsic benefits and extrinsic constraints playing a role in the evolution of cooperative polygamy and plural nesting.

One factor that appears to be of particular importance to several joint-nesting systems is the advantage in acquiring territories or other critical resources gained by coalition formation. For example, male lions (*Panthera leo*) have higher expected lifetime reproductive success in larger coalitions due primarily to an increased probability of gaining access to a pride of females (Koenig, 1981c; Packer et al., 1988). Other advantages, including longer residency and access to larger prides, confer lesser benefits. Coalition formation leading to increased access to resources (usually territories) have also been reported in pukeko *Porphyrio porphyrio* (Craig, 1984), green woodhoopoes (Ligon and Ligon, 1979, 1988), and acorn woodpeckers (Hannon et al., 1985; Mumme et al., 1988). This benefit can be considered an extrinsic constraint leading to group formation, since the advantage gained is that of acquiring an opportunity to breed, not in reproduction or survivorship per se (Koenig, 1981c). Why such extrinsic constraints lead to coalition formation and joint-nesting in a few species, while apparently comparable constraints result in delayed dispersal and helping in others, is unknown.

At one level, the distinction between nonbreeding helpers that delay dispersal and cobreeders that share a mate within a social unit can be reduced to differing degrees of reproductive bias within a group (Vehrencamp, 1983). This view is supported by the occurrence of mate-sharing in species such as the stripe-backed wren, in which male helpers

were previously all believed to be nonbreeders (Rabenold et al., 1990). To the extent that this is widespread, delayed dispersal/helping and plural nesting can perhaps be considered on the same continuum, with the latter occurring when demographic pressures are even higher than those leading to the former (e.g., Fitzpatrick and Woolfenden, 1986; but see Koford et al., 1986).

Alternatively, nonbreeding helpers and cobreeding may be distinct phenomena selected by independent sets of ecological factors. If so, there is currently no consensus concerning the conditions that promote one kind of cooperative breeding over another, much less the conditions leading to joint-nesting in some species and plural breeding in others.

Sex bias among helpers. There is as yet no satisfactory general explanation for the sex bias found among helpers in many species. Two general classes of hypotheses exist. Charnov (1981) suggested that the tendency for one sex or the other to act disproportionately as helpers is caused by sexual asymmetries in relatedness resulting from EPCs by males or from intraspecific parasitism by females. For example, assuming that egg dumping by females is rare and that EPCs by males are not, females will be more closely related to their own offspring than to broodmates, while males will be more closely related to broodmates than to young in their own nest, some of which they will not have fathered. Consequently, males receive relatively greater indirect fitness benefits by delaying dispersal and helping to raise siblings compared to dispersing and breeding independently. In the context of the delayed-dispersal threshold model, this hypothesis proposes a sex difference in the fitness differential between early and delayed dispersal: males experience a smaller differential than females because the higher probability of being cuckolded results in a lower benefit to independent breeding.

To the extent that the above scenario is likely, Charnov's (1981) argument can explain why there is a sex bias toward males among individuals that delay dispersal and remain as helpers in some species. Confirmation of this argument is dependent on finding a correlation between the sex bias in helpers

and the incidence of EPCs and egg dumping within cooperative breeders, as determined by parentage analyses. Particularly good tests would come from examination of species in which helpers are predominantly females rather than males, as is true for common crows (Caffrey, 1991) and small-bodied social canids (Moehlman, 1986). This latter taxon is particularly interesting from this perspective, as comparative data show that the sex ratio of helpers covaries with body size: helpers are predominantly or exclusively females in small-bodied species, approximately even in several medium-sized *Canis*, and predominantly males in larger taxa (Moehlman, 1986).

The second class of hypotheses for a sex bias among helpers focuses on the relative costs of delayed dispersal. For example, male Florida scrub jays are more likely to either inherit their natal territory or breed adjacent to their natal territory and thus stand to benefit more than females by delaying dispersal and helping; this is in fact the pattern documented by Stallcup and Woolfenden (1978). Unfortunately, there is an element of circularity in this argument: Do males help more because they are philopatric or are they philopatric because they help more? In any case, this correlation does not appear to generalize to other species; in green woodhoopoes, for example, males are more philopatric, as in Florida scrub jays, but there is no clear asymmetry in helping behavior between the sexes (Ligon and Ligon, 1979).

Several additional hypotheses for sex biases in delayed dispersal and helping behavior are discussed by Koenig et al. (1983) and Woolfenden and Fitzpatrick (1986). None provides a general explanation for the variation in this parameter observed in cooperative breeders. For species in which only one sex (generally males) delays dispersal and help, the nagging question remains: How can the conditions leading to delayed dispersal act on one sex but not the other (Walters, 1990)?

Geographic bias in cooperative breeding. Lack (1968) was apparently the first to point out the surprisingly high proportion of birds (estimated as at least 22% of passerines; Russell, 1989) that exhibit cooperative breeding in Australia. Several subsequent authors have noted or attempted to explain this pattern,

including Harrison (1969), Dow (1980), Brown (1987), Ford et al. (1988), and Russell (1989).

Russell (1989) pointed out that virtually the entire Australian continent has not been exposed to extremes of cold and seasonal drought since at least the mid-Miocene, 15 M.Y.B.P. Consequently, the Australian avifauna never developed the large-scale migrations characteristic of Europe and North America. Given that cooperative breeders are generally nonmigratory (Brown, 1974) and are often found in habitats where resources do not show marked seasonal fluctuations (Ford et al., 1988), this situation may at least provide the setting for the subsequent evolution of such a high incidence of cooperative breeding. This cannot be the whole story, however, since there are still many noncooperative breeders in Australia, and even members of the same genus living sympatrically may differ in their social organization (Ford et al., 1988; Russell, 1989).

Another relevant factor may be the phylogenetic history of the Australian avifauna. Russell (1989) and Edwards and Naeem (in press) have analysed the phylogenetic relationships of cooperatively breeding Australian passerines from a cladistic perspective; they suggested that the high proportion of cooperative breeders in the Australian avifauna may in part be a consequence of diversification among a relatively smaller number of lineages displaying this behavior. In part, this conclusion begs the question of why cooperatively breeding lineages have been so much more successful in Australia than elsewhere, and thus does not resolve the mystery. Nonetheless, the analyses of Edwards and Naeem (in press) make it clear that assessing the importance of phylogeny to the distribution and occurrence of cooperative breeding is an important challenge for the future.

The relationship between the social unit and the mating system. It has generally been taken for granted that the birds breeding in a particular social unit are group members. Recent electrophoretic work by Brooker et al. (1990) on splendid fairy-wrens, however, has shown that at least 65 percent of offspring in their population were apparently fathered by males outside of the group. Thus, as has been docu-

mented in numerous apparently monogamous species (Westneat et al., 1990), there is a potential discordance between the apparent and the genetically effective mating system in cooperative breeders.

In the case of the splendid fairy-wrens, this revelation calls into question the extraordinarily high incidence of apparent incest that had been reported earlier based on group composition (Rowley et al., 1986). Similar discoveries in other species as a result of modern molecular analyses (e.g., Burke et al., 1989; Rabenold et al., 1990) could have profound effects on our understanding of not only the mating system within groups of cooperative breeders, but also on our estimates of the costs and benefits of the different behavioral strategies observed in these complex systems.

CONCLUSIONS

The basic factors important to delayed dispersal were identified over 25 years ago by Selander (1964). Work since then has progressed in terms of understanding the demographic conditions correlating with delayed dispersal, but we still know relatively little about the ecological conditions promoting this phenomenon in some species, while constraining options such as floating in others.

Given the complexity and interrelatedness of the factors potentially influencing alternative dispersal strategies, no single factor is likely to explain delayed dispersal and helping behavior in all cooperative breeders. Indeed, the five factors identified here, including population density, fitness differential between delayed dispersal and dispersal/breeding, floater fitness, distribution of territory quality, and spatiotemporal environmental variation, all play an important, often interacting, role in determining the likelihood of delayed dispersal and cooperative breeding. The delayed-dispersal threshold model provides a framework that can aid in identifying key factors differing between closely related taxa exhibiting contrasting dispersal patterns among their offspring. Measuring the parameters needed to examine the model quantitatively is a key challenge to future researchers.

Detailed long-term studies of cooperative breeders will continue to add important clues to the puzzle of delayed dispersal, particularly if combined with experimental manipulations (e.g., Zack and Rabenold, 1989; Pruett-Jones and Lewis, 1990; Komdeur, 1991; Walters et al., in press). In addition, we advocate three kinds of studies. First are experimental tests of specific ecological factors important in the delayed-dispersal threshold model. Second are studies of noncooperatively breeding populations, either with or without close relatives that are cooperative breeders, focusing on what constraints to independent reproduction exist and why they do not result in delayed dispersal. Examples of such studies currently include those on *Lanius* shrikes (Zack and Ligon, 1985a, 1985b), *Aphelocoma* jays (see above and Carmen, in press), the various tits (genus *Parus*) (e.g., Ekman et al., 1981; Smith, 1984; Ekman, 1988; Matthysen, 1990), and banner-tailed kangaroo rats (Jones et al., 1988; Waser, 1988). Third are studies of intraspecific variation in group size and composition of cooperative breeders in relation to local habitat gradients and patchiness. Little work along these lines has been performed, yet such studies hold considerable promise for yielding insights into the environmental correlates of delayed dispersal and cooperative breeding.

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