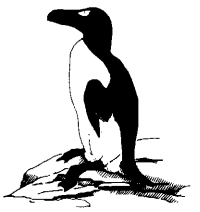
The Auk
A Quarterly Journal of Ornithology
Vol. 118 No. 1 January 2001



The Auk 118(1):1–10, 2001

PERSPECTIVES IN ORNITHOLOGY

DELAYED DISPERSAL: LIVING UNDER THE REIGN OF NEPOTISTIC PARENTS

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THE INCLUSIVE FITNESS concept (Hamilton 1964) formulated consequences of social behavior in gene equivalents. In doing so, it enabled fitness consequences of social behavior to be understood within the framework of genetic inheritance of traits. Delayed dispersal of birds was one system where the inclusive fitness concept was put to test. The key issue was to understand how delayed dispersal could be reconciled with evolution through natural selection, when retained offspring forego personal reproduction while they remain in the natal territory (e.g. Skutch 1961).

Cooperative breeding seems to have a secondary role for the maintenance of delayed dispersal, although 96% of bird species where the offspring remain with their parents into adulthood to form family groups also breed cooperatively (Emlen 1995). Although that association between delayed dispersal and cooperative breeding indicates that delayed dispersal is a permissive factor for the maintenance of cooperative breeding, there is not necessarily a causation going in the opposite direction. Cooperative breeding can be seen as an independent decision, and as such it is a consequence rather than a cause of delayed dispersal (Brown 1987, Stacey and Ligon 1987, Koenig et al. 1992, Emlen 1994, Hatchwell and Komdeur 2000), which is consistent with the observation that dispersal can be delayed without the retained offspring engaging in reproduction. Even if some of the retained offspring in a species participate in cooperatively breeding units, there are usually a substantial fraction of them that do not engage in help-at-the-nest, and only a few species like the White-winged Chough (*Corcorax melanorhamphus*) can be classified as an obligate cooperative breeder (Brown 1987). Even stronger support for the fact that delayed dispersal does not require any involvement of retained offspring in cooperative breeding comes from a number of species where retained offspring, as a rule, never help (Gayou 1986, Veltman 1989, Birkhead 1991, Ekman et al. 1994, Newton et al. 1994, Walls and Kenward 1996, Green and Cockburn 1999, Robinson 2000). Therefore, it seems that the maintenance of delayed dispersal requires an explanation that does not have to resort to fitness gains of cooperative breeding (see also Hatchwell and Komdeur 2000).

UNRESOLVED ISSUES

The fact that cooperative breeding should not be essential for delayed dispersal is consistent with the view that the behavior of remaining in the natal territory is maintained as a product of ecological constraints on dispersal options. Constraints can come in different forms such as lack of mates (Rowley 1981, Pruett-Jones and

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Lewis 1990), or high risks involved with dispersal (Emlen 1982). Most attention has been focused on a constraint in limited access to habitat in territorial species (Selander 1964, Brown 1969, Koenig and Pitelka 1981, Emlen 1982, Emlen and Vehrencamp 1983). Populations have restricted ranges, and the question of an ecological constraint in lack of vacant habitat (habitat saturation) therefore is reduced to a matter of the quality of unoccupied habitat (Brown 1969, Koenig and Pitelka 1981, Stacey and Ligon 1991). The offspring should gain from dispersing only as long as unoccupied habitat is of sufficiently high quality to be suitable and offer better conditions than what can be gained in the natal territory (Brown 1969). There is now also a growing insight in the role of variation in habitat quality in shaping dispersal strategies. There is tangible evidence showing that retained offspring postpone dispersal while they wait for territorial vacancies of high habitat quality (Zack and Ligon 1985, Komdeur 1992). Still, that evidence for the role of habitat quality does not mean that delayed dispersal is well understood (Heinsohn et al. 1990). Despite its apparent explanatory power, the concept of an ecological constraint in habitat saturation leaves several questions awaiting to be resolved, including (1) How can one account for the absence of delayed dispersal in species living in saturated habitats? (2) Where to wait for a vacancy, that is, why forego dispersal rather than to disperse and queue for vacancies in a territory of higher quality? (3) How can one explain that delayed dispersal is found predominantly among species with a life-history characterized by low adult mortality, low fecundity, and deferred maturity?

Dispersal in a Saturated Habitat

It is not clear how habitat saturation can account for the lack of delayed dispersal in species, which apparently experience an ecological constraint in accessing habitat that is as severe as in species with cooperative breeding (Brown 1969, Stacey and Ligon 1991, Koenig et al. 1992). That lack of generality in the ecological constraints approach was recognized by Brown (1969). Still, studies of the role of habitat saturation with respect to the timing of dispersal have been confined almost exclusively to studies of cooperative breeders with delayed dispersal (e.g. Brown 1987, Emlen 1997), whereas a critical test by Popperian philosophy should aim for systems that falsify the hypothesis to resolve why the hypothesis fails (Popper 1968). It is now well documented that the habitat saturation model fails to predict the absence of delayed dispersal in several cases including temperate regions parids (genus *Parus).* Removal experiments not only provided compelling evidence for habitat saturation in several parid species (Ekman et al. 1981, Ekman 1989), but additionally, their social system shares a suite of features with species that delay dispersal and are cooperative breeders. Several of temperate-region tits live in small, coherent, and sedentary groups occupying exclusive territories (Goodbody 1952, Dixon 1956, 1963, 1965; Weise and Meyer 1979, Ekman 1979, 1989; Nilsson and Smith 1985, Matthysen 1990) just as the overwhelming majority of cooperative breeders (Emlen 1995). The failure to provide an explanation for the lack of delayed dispersal in the genus *Parus* is a challenge to the ecological constraints model that has rarely been acknowledged (but see Stacey and Ligon 1991, Koenig et al. 1992), let alone resolved.

Where to Wait

Role of parents.—The trade-off nature of dispersal decisions, which was implicit in Brown's (1969) criterion that dispersal options have to be "suitable," is now widely recognized (e.g. Stacey and Ligon 1991, Emlen 1994). Dispersal is governed not only by constraints on access to resources elsewhere, but should be delayed when the natal territory offers benefits that either are higher than, or cannot be gained, elsewhere (benefits of philopatry; Stacey and Ligon 1991). Although identification of the role of habitat quality for the timing of dispersal recognizes the trade-off nature of dispersal decisions, its focus on habitat quality alone may be too simplistic. Variation in habitat quality is not a feature that is unique to species with delayed dispersal and cooperative breeding. Furthermore, a constraint on access to high quality habitat elsewhere does not preclude there also being other reasons for postponing dispersal where the benefits cannot be coined in terms of habitat quality.

Remaining in the natal territory, as a rule, entails that the offspring associate with relatives,

and parents in particular (Skutch 1961, Brown 1987, Emlen 1995). Offspring are the evolutionary currency of their parents, which have an interest in promoting the reproductive success of their offspring. Therefore, the consequences of dispersal are not only an issue for the offspring, but resolution of the cost–benefit tradeoff concerning the timing of dispersal should include the parents and their response to the presence of offspring into adulthood (Ekman and Rosander 1992, Cockburn 1996). Almost three decades after Trivers (1974) recognised the parent–offspring conflict, its role for how families resolve the dispersal decision remains to be explored. Field observation confirm that parents do have a role in the timing of dispersal, most obviously when parents enforce dispersal. In some species with delayed dispersal, such as the Gray Jay (*Perisoreus canadensis*) and the Green Jay (*Cyanocorax yncas*), the offspring are evicted by their parents at the onset of the breeding season the year after hatching (Gayou 1986, Strickland and Ouellet 1993). Although retained offspring from the previous breeding season are then evicted, it is implied that they have been tolerated so far.

Parental nepotism.—Involvement of parents in promoting delayed dispersal must by necessity be more subtle than enforcing dispersal. It is biologically unrealistic that the parents enforce delayed dispersal. Rather, parents have to promote postponed dispersal by encouraging their offspring to remain. Parents are unlikely to be able to affect conditions elsewhere, and the encouragement has to be based on providing benefits in the natal territory by offering conditions that are better than what the offspring can gain elsewhere. There are different options available to parents with respect to how to promote the prospects of independent breeding of their offspring. Brown and Brown (1984) emphasized that parents could assist their offspring in the acquisition of a breeding territory and reproductive status. They called that mechanism "parental facilitation."

To become breeders, the offspring have to survive while they are waiting for a suitable breeding opportunity to emerge, and the offspring should delay dispersal if they survive better in the natal territory than elsewhere (Brown 1978). The potential role of survival prospects while queuing for the timing of dispersal has not been fully recognized because of the choice of evolutionary currency. Evolutionary consequences of living in family groups have conventionally been evaluated in reproductive equivalents. However, the potential of survival prospects to account for delayed dispersal is apparent with a multiseasonal approach, where reproduction is not the sole fitness component (Kokko and Johnstone 1999). The model of Kokko and Johnstone shows that survival prospects weigh heavily in the dispersal decision, and that it is theoretically fully conceivable for the offspring to benefit from delayed dispersal even if they should not contribute to reproduction at all. That model provides a theoretical confirmation of the suggestion that delayed dispersal does not require fitness gains of cooperative breeding (Brown 1987, Emlen 1994).

A parental behavior that enhances the access to food for retained offspring should have a direct bearing on starvation risk, and it is now known for several species that parents do concede food resources to retained offspring in the nonbreeding season. Parents allow their offspring access to food that is denied unrelated individuals (Verbeek and Butler 1981, Barkan et al. 1986, Ekman et al. 1994, Pravosudova 1999), but they also protect their offspring from aggression by competitors on feeding grounds (Scott 1980). The parental behavior of conceding resources to the offspring qualifies as nepotism in that it is "favoritism shown . . . relatives" (Webster's International Dictionary, 1976). Nepotism is a behavioral mechanism of kin selection, and all favoritism of kin is nepotism (Sherman 1980). What is special with nepotism is the emphasis on the difference in how kin are treated relative to unrelated individuals, and a nepotistic relationship defines how the parent–offspring relationship governs the access to food in foraging bird flocks. However, nepotism must not be confined to food resources, but so far there are no studies of whether alarm-calling in response to predators is nepotistic in birds, like it is known to be in some mammals (Sherman 1977, Cheney and Seyfarth 1990). That opportunity for the parents to offer benefits to offspring remaining in the natal territory remains to be explored in birds.

Any evolutionary consequences of parental nepotism must be derived from fitness consequences, and there is now evidence in the Si-

berian Jay (*Perisoreus infaustus*) suggesting that an association with nepotistic parents enhances first winter survival (Ekman et al. 2000). Inasmuch as nepotistic parental behavior promotes delayed dispersal by enhancing offspring fitness, delayed dispersal represents an "extended parental investment" (Zahavi 1974, Ligon 1981, Brown and Brown 1984, Fitzpatrick and Wolfenden 1986, Ekman and Rosander 1992).

Decoupling queuing and associating with the parents.—Benefits of parental nepotism do not exclude ecological constraints such as a limited access to high quality habitat elsewhere. Rather, ecological constraints promoting delayed dispersal are reinforced by benefits gained from remaining in the natal territory. Equally important, the concept of "extended parental investment" can provide a solution to why offspring choose to remain in the natal territory, a question that is not resolved by constraints on independent reproduction. An offspring that responds to ecological constraints on independent reproduction by waiting for a better option than the ones currently available often does so in association with the parents, like in cooperative breeders. An association with the parents could be seen as a by-product of delayed dispersal, but there is nothing that necessitates that the offspring wait in the natal territory. Even if the offspring should have to wait for a breeding opportunity to emerge, this does not provide an answer to the question of where to wait. Rather, the response to a lack of breeding opportunities is composed of two separate decisions: (1) whether to postpone personal reproduction and wait for a "suitable" breeding opportunity of sufficiently high quality, and (2) whether to associate with the parents while waiting for a breeding opportunity. Delayed dispersal therefore suggests that an association with the parents has a value in itself to the offspring. The fact that "home" has a special status has not traditionally been incorporated in models of the evolution of dispersal. Recently, Kokko and Lundberg (in press) have shown that this factor strongly enhances the prospects for delayed dispersal.

Where an ecological constraint (e.g. lack of high quality habitat) fails to account for delayed dispersal, parental nepotism is able to provide an answer to why the offspring should wait in the natal territory rather than disperse to queue in another territory where the habitat is of higher quality. Given variation in habitat quality, why do the offspring not disperse to wait for a vacancy in a territory of better habitat quality? One reason could be that the parents, by definition, can be found only in the natal territory. The opportunity for offspring to associate with nepotistic parents is a true "benefit of philopatry," which can be gained only in the natal territory. If it were not for parental nepotism, offspring should do better by shifting to a territory of higher quality, in line with an ideal free distribution (Fretwell and Lucas 1970, Sutherland 1996). Given that the quality of an alternative is sufficiently high, dispersal would not be hindered even by crowding. That points to the importance of the nature of the parent–offspring relationship for how the dispersal decision is resolved. The presence of nepotistic parents would make the difference between the natal territory and other territories of higher quality as a place to queue.

Without the benefit of associating with the parents, the offspring could queue anywhere, or float, and that is exactly what they do in several species. Decoupling the decision of waiting for a breeding opportunity of high quality from associating with the parents allows the role of habitat quality and nepotism to be evaluated independently. Such a decoupling of the two decisions could resolve the long-standing problem of accounting for dispersal of species, although their habitat is saturated (Brown 1969). The key difference in the social behavior of parids, in contrast to species with delayed dispersal and living in family groups, is not found in the response to habitat saturation per se, but in the association to the parents. Whereas temperate region parids do wait for a vacancy as subordinate flock members (Ekman et al. 1981, Ekman 1990, Hogstad 1987), they do not form flocks with their parents (Ekman 1989, Matthysen 1990), unlike species that delay dispersal (Brown 1987, Emlen 1995). It is therefore possible that the explanation for why parids neither delay dispersal, nor form family groups, is to be found in parent–offspring relationships. Then why should parids not have an incentive to associate with their parents? Is it so that parents could be nepotistic in some species but not in others?

The logic of parental concession.—The notion that delayed dispersal has an element of parental care emphasizes a cooperative relationship,

in contrast to a competition-oriented view of parent–offspring relationships (Emlen 1982, Emlen and Vehrencamp 1983). Parents provide benefits, which prompt the offspring to postpone dispersal, and the decision to delay dispersal would be decoupled from any participation of the offspring in reproduction. That view of delayed dispersal as a form of parental care is consistent with the conclusion that cooperative breeding is not a necessary condition for delayed dispersal. Furthermore, it is consistent with observations that dispersal can be delayed although the offspring do not help.

An extended parental investment is based on the fact that it is in the interest of the offspring to remain in the natal territory and the parents permit it. However, the concession of food shows that parents do more than simply permit it. They augment conditions for their offspring and actively promote postponement of dispersal. What is good for the survival of the offspring is also in the interest of the parents, because surviving offspring can produce grand-offspring. The parents will therefore gain just from that retained offspring remain alive. Still, a nepotistic behavior has to be reconciled with the fact that parents value their own survival and reproduction higher than that of their offspring (Trivers 1974).

Trading parent and offspring survival.—To resolve what is seemingly a conflict of interest between how parents value their own well-being against that of their offspring, it is important to realize the probabilistic nature of survival. Survival is never certain, but the probability of escaping starvation increases with access to food and energy reserves (McNamara and Houston 1990). Therefore, behavior will be related to survival prospects in a quantitative way. The upper limit to survival prospects entails a nonlinearity where the magnitude of fitness gains in enhanced probability of survival from resources level off as it approaches unity. The opportunity for parents to gain from conceding does not depend on the level of resource abundance or survival as such, but it is a product of the change in survival prospects with resources. The slope of this function is, however, linked to absolute values for survival probabilities (Fig. 1). Therefore it is parents with high survival prospects that can gain from conceding.

To explore how diminishing returns from food resources exacted in survival prospects could promote parental nepotism in concession of food resources, Ekman and Rosander (1992) theoretically analyzed a situation where a parent and offspring have to survive from a common and limited resource. An extended parental investment in concession of resources (called "prolonged brood care" by Ekman et al. 1994) is expressed as parental nepotism, which allow the offspring to consume resources that the parents would have been able to control. The asymmetry in fitness costs and benefits from such a resource-transfer between parents and offspring can be illustrated by the biologically realistic assumption that parents, being more experienced foragers, can achieve a lower risk of starvation (higher survival) than inexperienced offspring from the same resource abundance. An alternative approach with similar consequences would be that parents are in control of a major share of resources. Given that difference in survival prospects, there is scope for parents to make an inclusive fitness gain from conceding resources they control to the offspring (Fig. 1A), and the enhanced offspring survival would promote delayed dispersal.

Life-History and Delayed Dispersal

Delayed dispersal is more prevalent in species with low adult mortality, low reproductive rates, and deferred maturation. That link between the life history and a disposition to delay dispersal has been suggested (Brown 1987) and the empirical support for that hypothesis has been reinforced by phylogenetic analyses (Arnold and Owens 1998). Hence, it must be possible to reconcile any explanation for delayed dispersal with that correlation. However, descriptive patterns of comparative analyses will not in themselves establish causation. Furthermore, it is not necessarily obvious that life-history characteristics, like low reproductive rates, should result in a habitat saturation that is more severe than for species with high reproductive rates and without delayed dispersal as with, for instance, several temperate-region *Parus* species with clutch sizes in the range of 8 to 10 eggs (Bent 1946, Cramp and Perrins 1993). Still, any explanatory model must produce a distribution of delayed dispersal among taxa,

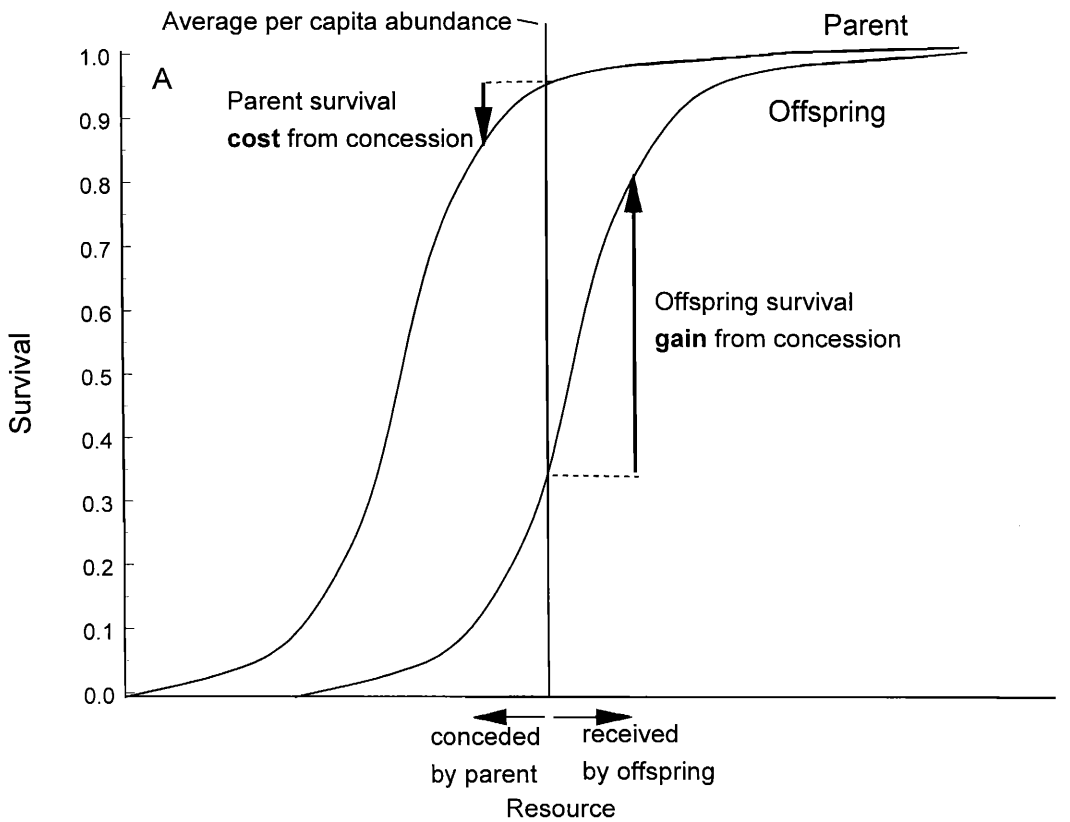

FIG. 1. The asymmetry in survival consequences from parental nepotism in concession of food resources to an inexperienced or subordinate offspring. The fitness functions for parents and offspring as a function of resource abundance is expressed as the probability of escaping starvation by having more energy reserves than a critical survival cutoff, assuming that food encounter is a Poisson process (=survival). The amount of resources that are conceded by parents equals amount received by the offspring. Notice that offspring benefits have to be devalued by degree of relatedness (r; here 0.5) to give the inclusive fitness gain from concession to parents. The effect of resource abundance is illustrated by two examples: (A) high abundance, and (B) low abundance. (A) Concession of food pays in inclusive fitness; high food abundance with potential for high parental survival prospects produces a survival asymmetry with a gain to offspring (recipient) which exceeds cost the parent (donor). (B) No inclusive fitness gain from concession of food; low food abundance and low parental survival produces a survival asymmetry where cost to the parent (donor) outweighs benefit to offspring (recipient). (Modified after Ekman and Rosander 1992).

either directly caused by life-history traits or not, which is consistent with the observed pattern in life-history correlates.

Parental nepotism in concession of food may not only provide the offspring with a survival benefit that promotes delayed dispersal. It is apparent that this potential to make a gain from nepotism is available only to parents with high survival prospects. Theory predicts that parents should be willing to provide prolonged brood care, promoting delayed dispersal, only when their own survival prospects are high (Fig. 1A). Two factors curtail the potential for an inclusive fitness gain: (1) The asymmetry with survival gains (to offspring) that exceed costs to parents with high survival prospects is reversed at low parental survival prospects (see Fig. 1B). (2) Parents should concede resources only when their own survival prospects are sufficiently higher than those of the offspring, whereas offspring survival has to be devalued by the degree of relatedness (here 0.5) to give the marginal inclusive fitness gain to parents.

Hence, the theoretical prediction for when parents should be nepotistic is consistent with

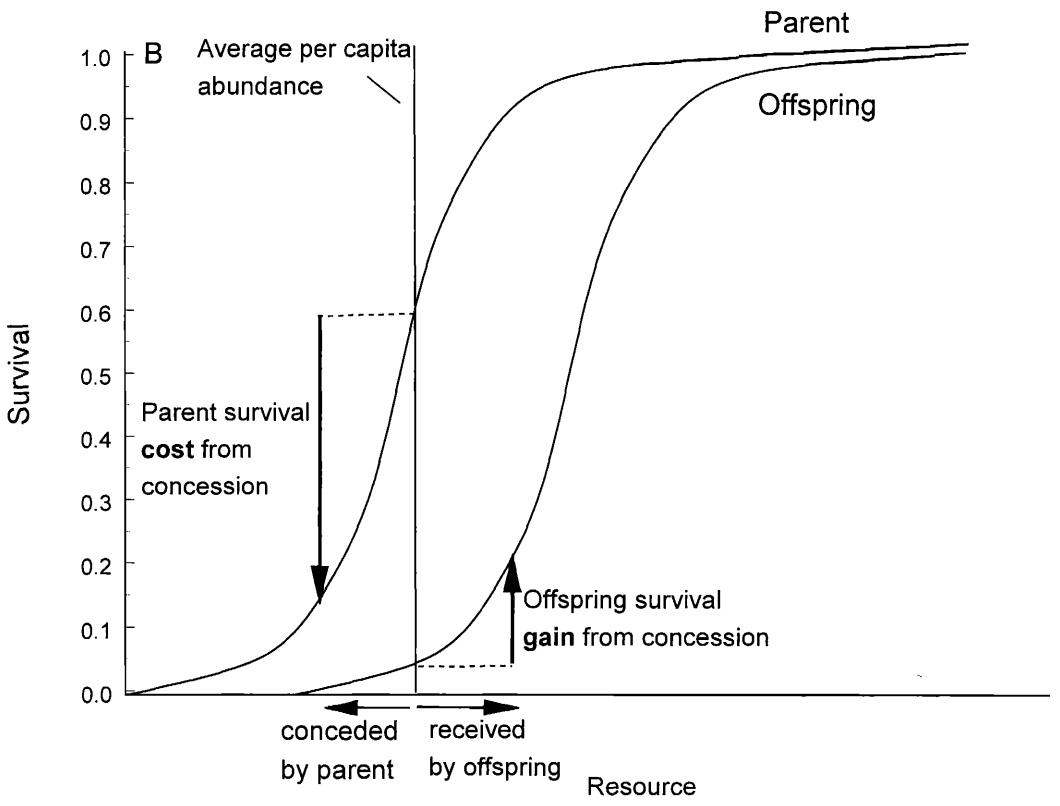

FIG. 1. Continued.

life-history correlates. Furthermore, a causal relationship between life-history and parental nepotism would be able to account for why species like parids do not delay dispersal, although they experience a saturated habitat. Access to food is critical to survival prospects of parids (Jansson et al. 1981, Brittingham and Temple 1988), which furthermore are low compared to species with delayed dispersal (Arnold and Owens 1998). Therefore, parid parents may lack the incentive for nepotistic sharing of food, which would entail that the offspring have nothing to gain from waiting in association with their parents.

Theory shows that a cost in reduced personal survival from conceding food resources is critical to the willingness of parents to concede resources (Ekman and Rosander 1992). That cost can be outweighed by the inclusive fitness gain to their offspring only for parents with high survival prospects (Fig. 1). The same prediction has been made with different modeling techniques (Taylor 1988, McNamara et al. 1994), suggesting that the prediction is robust to assumptions. Apart from that theoretical robustness, the inherent strength of the "prolonged brood care" model can be summarized as (1) the predicted species difference, in the timing of dispersal in response to parent behavior, is consistent with how delayed dispersal is correlated to certain life-history traits. (2) Parental nepotism can be accommodated in a trade-off approach to dispersal decisions as an intrinsic benefit when dispersal requires a suitable option. (3) There is a behavioral mechanism for how the parents are nepotistic. (4) The occurrence of nepotism can be tested by comparing if parents concede resources to offspring but not to non-related flock members.

So far, there are few examples of species where nepotistic parents share resources with retained offspring in the nonbreeding season (Barkan et al. 1986, Ekman et al. 1994, Pravosudova et al. 1999). Still, those examples demonstrate that the behavior is a reality. Furthermore, the scarcity of examples has to be seen in

the light of a bias in interest towards reproductive consequences of species with delayed dispersal and cooperative breeding. A nepotistic behavior in that parents concede resources is a "nonbehavior" characterized by a lack of aggressiveness when access to food is controlled through despotic behavior. It is a less conspicuous behavior than the more spectacular cooperative breeding, and it could therefore easily be overlooked, despite its potential importance to the decision to postpone dispersal and maintain an association with the parents. Concession is based on the fact that parents refrain from claiming their priority to resources. Confirmation of such nepotism becomes evident only in a systematic comparison of social relations within nonbreeding flocks.

ACKNOWLEDGMENTS

Jacob Höglund, Hanna Kukko, and Steffan Ulfstrand read the manuscript and suggested many improvements. The study was supported by grants from the Swedish Natural Science Research Council (to J.E.)

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