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Delayed Dispersal: Youth Costs Carry Lifetime Gains

An analysis of reproductive success in the green woodhoopoe *Phoeniculus purpures* challenges the view that delayed dispersal is costly. Females delaying dispersal for longer had more reproductive events in life and higher lifetime production of offspring.

Jan Ekman

The carrying of identical genes by descent renders cooperation with relatives an alternative route to personal reproduction and the transfer of genes into future generations in multigenerational families, but cooperation comes at a cost. Relatedness does not just breed cooperation — reproductive conflict can be rife within families. Although offspring are evolutionary assets to parents, given their capacity to produce grandchildren, reproductive conflict and incest taboos often prevent them from reproducing as long as they stay together [1], and they eventually have to disperse and leave their parents to breed. Delayed dispersal, which maintains family association and allows complex social behaviours such as cooperative breeding, thus comes with an evolutionary cost in that retained offspring forego opportunities for personal reproduction [2]. Yet, an analysis of the reproductive performance over the entire lifetime of the cooperatively breeding green woodhoopoe *Phoeniculus purpureus* (Figure 1), reported recently in *Current Biology* [3], provides evidence challenging the view that delayed dispersal is costly. Accepting a cost early in life can come with compensatory gains later in life that give delayed dispersal a selective advantage.

Attempts to assess the adaptive gains of delayed dispersal have generally been confined to the time when the offspring still associate with the family, and to cooperative breeding in particular. Yet, any gains to retained offspring from cooperative breeding have proven small and insufficient to compensate for the loss of personal reproduction [4]. By measuring the lifetime consequences of delayed dispersal, Hawn *et al.* [3] were able to assess the reproductive performance of woodhoopoes in a way that is consistent with the basic tenet of life history theory which assumes that costs and benefits do not have to operate simultaneously. Unlike in studies with a perspective of adaptive benefits confined to the return from cooperative breeding within multigenerational families, the woodhoopoe study [3] shows that selective advantages can be delayed until after independence and come in the form of enhanced personal reproduction.

Given the weak adaptive benefits from cooperative breeding, delayed offspring dispersal has been reconciled with the cost of lost reproduction by assuming there is a lack of opportunities for independent breeding, rather than invoking an adaptive behaviour. The behaviour to postpone dispersal involves a waiting time, with dispersal opportunities constrained by ecological conditions. On the face of it, offspring should be better off if they could leave. The 'ecological constraints' explanation for the formation of multigenerational families assumes that delayed dispersal is costly, and that costs and benefits operate simultaneously and are all contained within the time span when the offspring remain with their families. Once constraints are lifted, the offspring leave according to the tenets of the 'ecological constraints' [5,6]. The enhanced lifetime reproduction of female green woodhoopoes when they delay dispersal for longer, reported by Hawn *et al.* [3], challenges the view that delayed dispersal should be costly.

In an evolutionary perspective, it is reproductive performance over the lifetime that counts, and viewing any adaptive returns from delaying dispersal as restricted to the time of remaining within the family, and from cooperative breeding in particular, will forego the lessons from life history. To address the selective consequences of delaying dispersal, the team studying the African green woodhoopoe [3] took the stance of measuring reproductive performance over the entire lifetime, while comparing against timing of dispersal. They found that females had a longer breeding career, and therefore produced more offspring over their lifetime, when they had postponed independence for longer, unlike what was expected if they had

Figure 1. A green woodhoopoe *Phoeniculus purpures*.
Photo: Claire Spottiswoode.

merely been constrained from a dispersal allowing them to breed independently. Such a selective advantage of delaying dispersal is consistent with behaviour during the actual dispersal process in other species. Delayed dispersal is the preferred option in sibling rivalry over holding the position as retained offspring [7,8].

Hawn *et al.* [3] found no evidence that females with delayed dispersal acquired better territories and therefore had longer breeding careers. Green woodhoopoes have proven susceptible to night cold and the wall thickness of hollows used for the night rest has proven to be a critical territory quality [9], but there was no difference in hollows for females with breeding careers of different lengths. So if external factors cannot explain the differences in lifetime reproduction, the state of females is another possibility. One cost of reproduction in a life history perspective is that it jeopardizes future reproduction by increasing the risk of mortality [10]. Starting to breed early as an inexperienced female might thus have carried larger risks, as reflected in their shorter reproductive career, while the selective advantage of delayed dispersal could have come through personal benefits in an alleviated reproductive cost. If so, delayed dispersal would have evolved as a life history trait selected through its effects for reproductive cost, rather than for the evolutionary gains of cooperation in breeding family units.

Only future studies can show the exact mechanism explaining why females with delayed dispersal reproduce better. Still, the delayed effect in enhanced personal reproduction after dispersal [3] makes it necessary to see the evolution of delayed dispersal and cooperative breeding in a life history perspective. This life history perspective has consequences for data relevant to delayed dispersal as well as field procedures. As a corollary it is not sufficient to base conclusions about adaptive gains from delayed dispersal merely on data on reproductive performance in cooperatively breeding groups. The performance as independent breeder matters.

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Mental Time Travel: Animals Anticipate the Future

Recent behavioral experiments with scrub jays and nonhuman primates indicate they can anticipate and plan for future needs not currently experienced. Combined with accumulating evidence for episodic-like memory in animals, these studies suggest that some animals can mentally time travel into both the past and future.

William A. Roberts

Important recent findings reported in *Nature* [1] and *Current Biology* [2] indicate that a species of corvid, the scrub jay, can anticipate a future need for a specific kind of food and store that food in advance of the future need. Even though scrub jays have no current hunger for pine seeds, for example, they will cache these seeds hours or even a day in advance of the time when they will hunger for them. These results, along with other experiments carried out recently with nonhuman