Forest fragmentation: another perspective

In his recent (and very favorable) review of our edited book, *Tropical Forest Remnants*[1], Egbert Leigh raised some issues of general interest to those who study the ecology of fragmented habitats. I would like to respond to two of these points, and propose a differing view.

First, I question Leigh's contention that, because of formidable taxonomic constraints, fragmentation researchers should focus on less-diverse, seasonal forests, rather than those of super-diverse regions like the Amazon, as is being attempted in the Biological Dynamics of Forest Fragments Project (BDFFP). The Amazon, in my view, is simply too extensive and important to ignore. Moreover, while it is true that the identification of over a thousand tree species in the BDFFP study area has been a massive challenge, there has been much progress in recent years. Important work on forest dynamics[2,3], biomass[4], regeneration[5,6], and phytosociology[7] in our fragmented landscape has recently appeared, or will soon appear, in major journals.

Second, Leigh suggests that the study of ecological interactions and distortions, revolving around plant communities, is needed to provide a 'unified, coherent understanding of the effects of forest fragmentation.' Such interactions could occur, for example, if certain pollinators or seed-dispersers declined in fragments, thereby leading to the eventual collapse of their dependent plant species, which then might cause a cascade of ecological changes affecting yet other species.

While this sounds useful and scientifically appealing, in practice there have been surprisingly few demonstrations of the importance of such higher-order interactions in fragmented habitats, especially given the prominent role that symbioses are known to play in tropical forests[8]. Indeed, one of the chapters in our book, in which Australian investigators invested several years in a failed attempt to detect the effects of loss of a keystone seed-disperser (the cassowary) on its dependent tree species, concluded that the study of such interactions was fraught with risk, and often prone to failure[9]. Given the inherent complexities and nonlinear behavior of many ecological interactions, I suggest that the nature, direction and magnitude of higher-order effects in fragmented habitats will often be extremely difficult to predict. Hence, while the study of higher-order interactions is likely to remain a useful arrow in the fragmentologist's quiver, we are far from ready to view it as a general paradigm for predicting the ecological consequences of fragmentation.

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Reply from E.G. Leigh

Laurance questions two remarks in my review of *Tropical Forest Remnants*. I said, in blatant hindsight, that Amazonian tree diversity has nearly paralyzed the Manaus forest fragment project, and, perhaps more excusably, that a tree-centered view is needed to attain a coherent view of forest fragmentation.

These two remarks are really one. I am a theorist, a story-teller. Even Gould and Lewontin[1] haven't broken my habit. To make a coherent story about tropical forest, *I* must center on trees: what landscape they make, how much they produce, how they avoid annihilation by herbivores, how they coopt animals, fungi, etc. into their service[2]. This story-telling approach allowed me to suggest a coherent explanation of tree species composition of minute 80-year-old islets in Panamá[3]. Has my love of a good story led me to criticize the Manaus project unjustly?

Only future research will decide. Nonetheless, lecturers know that requiring a story coherent enough to interest students and satisfy their questions provides a severe and probing test of a theory[4]. Good story-telling is *an* essential aspect of science. Moreover, Terborgh, the biologist who did most to reveal the secrets of Amazonian ecology[5,6], chose a tree-centered approach to understand the changes on islands created by Venezuela's Lake Guri. His results are promising[7]: although a similar approach failed in Australia[8], I would guess that Terborgh's Guri work will decisively influence future investigations of forest fragmentation.

My remark about the problems posed the Manaus project by Amazonian tree diversity is *not* a recommendation to ignore Amazonia. Rather, I think that understanding the consequences of forest fragmentation is inextricably linked to understanding the interrelationships maintaining the structure and diversity of intact forest.

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The evolution of coloniality: does commodity selection explain it all?

Recently, Danchin and Wagner[1] reviewed the different hypotheses for explaining the evolution of colonial breeding in vertebrates, concluding that no general framework has resulted after decades of research. As an alternative they proposed the 'commodity selection' approach: individuals could select colony sites by evaluating their quality through conspecific cues that combine the effects of all potential costs and benefits of coloniality. This is undoubtedly a promising path that will increase the understanding of some complex and unresolved aspects of coloniality. However, this single approach may misdirect further research efforts towards the study of the proximate causes of individual decisions, replacing the examination of costs and benefits – which could certainly distinguish the different pressures leading to coloniality.

Danchin and Wagner rejected the 'economic framework' (relationship of costs and benefits), because 'their balance is extremely difficult to assess'[1]. However, this balance is clearly obtained by calculating the lifetime reproductive success (LRS) of individuals breeding in different aggregation levels (solitary and in colonies of different size)[2,3]. This approach allows us to identify the optimal breeding strategy, whatever the costs and benefits involved. The only difficulty is that it requires long-term population studies for obtaining accurate components of individual fitness such as productivity and survival of parents and offspring, which are necessary for modeling LRS[3].

The identification of costs and benefits is difficult, sometimes because of the lack of exclusive predictions[1], but also because studies are usually of short duration. For example, the role of predation is dismissed as a factor leading to the existence of enormous seabird colonies breeding in predator-safe islands and cliffs[4], while the present-day location and size of these colonies could be the result of predation pressure in the past[5]. This pressure can be observed in recently established populations of some species[3]; in fact, many established seabird colonies disappear after predators gain access to them (e.g. Ref. 6).

According to Danchin and Wagner, coloniality is the result of multiple interacting costs and benefits, which may vary according to species, populations and individuals, and short-term studies testing a single hypothesis frequently lead to contradictory results. However, for the same reasons, contradictory results could also derive from the 'commodity selection' approach if researchers are focused on a 'wrong' cue. The authors propose reproductive success and potential partner quality as important conspecific cues for breeding patch (colony) selection. However, the role of current reproductive success on individual fitness could vary greatly between species with different life histories. For instance, in some territorial[7] and colonial species[3], predation largely determines LRS. In these species, evaluating the risk of predation in each patch could be more important than accurately evaluating breeding success[8]. As birds tend to abandon colonies the next year after a predation event, the number of birds at a colony early in the season could be a good indicator of predation-safety and a motor for conspecific attraction. On the other hand, in a number of colonial species, extra-pair fertilizations are negligible (e.g. Refs 9,10), so it seems unlikely that the pursuit of extra-pair copulations[11] has been a primary cause of coloniality in these species[2,3]. Obviously, testing the hypotheses of 'commodity selection' requires the identification of cues for each species, and probably populations, being then no more simple than the determination of costs and benefits.

The 'commodity selection' is not an alternative, but rather a complementary approach to the previous framework for studying the evolution of coloniality. The balance of coloniality as derived from LRS modeling allows us to identify the optimum aggregation level. The study of costs and benefits may determine the pressures responsible for the origin of these aggregations. On the other hand, the 'commodity selection' refers to mechanisms leading to individual decisions (where to breed and where to move to improve fitness), opening new perspectives for the comprehension of related ecological problems, such as breeding and natal dispersal and the delay of the first reproduction[12], both in colonial and territorial species.

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Reply from E. Danchin, R. Wagner and T. Boulinier

We are pleased with Tella *et al.*'s comment that 'commodity selection' offers a promising new approach for understanding some unresolved aspects of coloniality. Our review implies that animals may not be selected to breed colonially, but rather to choose commodities like breeding habitats and mates, which secondarily may have produced breeding aggregations. Tella *et al.*'s main argument is that commodity selection is a complement to the orthodox economic approach of measuring costs and benefits of high density breeding, rather than a substitute for it.

Our general response is to reiterate that the economic approach has failed to provide a general explanation of colony evolution, largely because the wrong questions have been asked. Indeed, when investigating the evolution of coloniality, we do not want to know whether it is better for an individual to breed in a bigger or smaller colony, but we want to understand the processes (rather than the benefits) that lead to breeding aggregations.

The estimation of the lifetime reproductive success (LRS) of individuals in a variety of colony sizes may produce information on colonial breeding[1], but this method cannot reveal the mechanisms of colony formation. If, for example, certain individuals choose small colonies that subsequently expand around them (both in the current and next seasons), then knowledge of their LRS in relation to their 'choice' colony size will not elucidate the processes of colony formation. Furthermore, LRS is unlikely to be the right measure of fitness, particularly in this context[2].

Our main point about reproductive success (RS) is that it is a cue that conspecifics can appraise to aid them in selecting breeding habitats and mates. Their ultimate and proximate processes meet: patterns of spatiotemporal variability of the environment (including the distribution of mates of heterogeneous quality) may have led to the evolution of habitat selection strategies that produce dynamic aggregations of breeding individuals[3]. Individuals that prospect for a breeding site for the next season may not need to know the actual causes of local reproductive failure or success (predation, etc.) this season. They only require information on the breeding performance of local breeders in a given year.

The discussion on predation underlines a classic problem when studying adaptation: current impact may be misleading, and a comparative study of coloniality showed that coloniality is positively associated with exposure of nests to predation[4]. But, the high current levels of predation cannot be used to argue that predation played a role in the evolution of coloniality. It may well be that some advantages of coloniality secondarily allowed species to nest in exposed situations[4]. Similarly, low frequencies of extra-pair paternity in colonial species cannot be used to argue that sexual selection plays a secondary role in the evolution of coloniality. The sexual selection (or 'hidden lek') hypothesis[5] predicts that the frequency of extra-pair copulation is the more direct variable explaining nesting aggregation. In support of this prediction, frequency of extra-pair copulations[6] was found to be higher in colonial species.

In this context, it is clear that long-term studies are important in allowing to relate the fate of individuals and their breeding distribution to the patterns of spatiotemporal variation of habitat quality, and of factors affecting it (e.g. Ref. 7). Experimental approaches are nevertheless necessary to demonstrate causality. The commodity selection framework prescribes the design of much-needed experiments to test predictions of habitat and mate selection in relation to aggregation (e.g. Refs 3,7, Table 1 in Ref. 8).

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Taking time with microevolution

In a recent *TREE* News & Comment article, Svensson compared rates of evolution in the fossil record to those observed in transplant studies[1]. Given the expanding interest in this approach, a

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