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# Forum

## Colonies as byproducts of commodity selection

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When ecologists examine a colony, they tend to ask, what are the benefits of breeding in aggregations? In contrast, when students of leks examine an arena of displaying males, they usually ask, what are the mechanisms that produce aggregations? Here we discuss the differences in these two approaches. The value of this distinction stems from the frustrating inability of decades of research to provide a general explanation of the widespread occurrence of colonial breeding. The traditional approach to studying coloniality is the measurement of costs and benefits of breeding in high density (Barclay, 1988; Brown and Brown, 1996; Emlen and Wrege, 1986; Hoogland and Sherman, 1976; Møller, 1987; Wittenberger and Hunt, 1985). Our aim is to illustrate how individuals can pursue adaptive strategies that result in their joining breeding aggregations without necessarily obtaining net benefits from the aggregation.

In a recent review (Danchin and Wagner, 1997), we identified a mechanistic approach to studying coloniality which synthesizes two new hypotheses. The ''habitat selection'' hypothesis proposes that animals imitate the breeding habitat choices of successful conspecifics to benefit from the same favorable environmental conditions as successful breeders (Boulinier and Danchin, 1997; Danchin et al., 1998). The sexual selection, or ''hidden lek,'' hypothesis proposes that males of monogamous, colonial species aggregate their nesting territories by the same mechanisms that cause males of lekking species to aggregate their display territories (Wagner, 1993, 1997). These two hypotheses share a single common assumption that is simple but heterodox to the study of coloniality; namely, that nesting aggregation may be merely a byproduct of many individuals selecting commodities such as habitat and mates, and not necessarily a benefit to the individuals that aggregate. The fact that the aggregation need not produce benefits does not argue, however, against using cost–benefit analyses, but rather argues for measuring the costs and benefits of specific decisions made by individuals that lead them to produce a pattern of aggregated breeding.

The issue of breeding aggregations fits into the more general problem of animal group sizes, which was solved by Pulliam and Caraco (1984) by applying the logic of the ideal free distribution. The main point of those authors is that group sizes may be byproducts of other factors, making it futile to search for optimal group sizes. Despite the success of that approach in other types of animal aggregations, the question of coloniality continues to be dominated by the search for optimal group size (e.g., Brown and Brown, 1996).

Here we illustrate how the processes of mate selection and breeding habitat selection can produce aggregation as a byproduct, without individuals necessarily benefiting from breeding in dense aggregations. First, let us consider the approach taken by some lek modelers to explain aggregations of males via processes of sexual selection. Leks are aggregations of males that females visit for copulation (Bradbury, 1981). One of the three principal models of lek evolution is the hotshot model, which proposes that less attractive males aggregate around the top male, or ''hotshot,'' to gain access to females that are attracted to him (Beehler and Foster, 1988). The hotshot model assumes that the aggregation of males is a byproduct of female and male behavior; none of the individuals in the lek benefits from aggregation, yet aggregation occurs. The model assumes three kinds of players: secondary males, the hotshot male, and females. The reason secondary males aggregate around the hotshot is to intercept females before they can obtain a copulation from the hotshot, and, in fact, courtship disruptions are sometimes the strongest correlate of copulation success (Pruett-Jones and Pruett-Jones, 1994; Trail and Koutnik, 1986; Wagner, 1992). Thus, hotshots who are capable of attracting females in the absence of other males will often lose mating opportunities to males that are aggregated around them. Females also suffer from the aggregation of less attractive males because they are disrupted from copulating with the top male. Thus, male aggregation is a byproduct of female behavior and may be costly to females. In this model, females do not search for leks, but rather for hotshots and, as a result, incidentally produce leks.

The question remains whether secondary males benefit from aggregation. Clearly, a secondary male can benefit by displaying near a hotshot. However, each individual male may suffer costs from the presence of other secondary males, who are all competing to intercept the same females. Secondary males, therefore, may not benefit from the presence of other secondary males. Thus, individuals of all three types may suffer net costs from the aggregating of others, yet they produce aggregation.

The above example does not contradict the use of a cost–benefit analysis but suggests the appropriate level at which to perform the analysis. For example, the benefit to females of searching for a mate in a lek outweighs the cost of aggression or disruption from secondary males. For secondary males, the benefit of some mating success obtained by displaying near a hotshot outweighs the cost of receiving aggression from other males. For the hotshot, the cost of losing some matings to secondary males might be outweighed by the cost of establishing a new display territory.

The example of the hotshot model is linked to the study of coloniality by the hidden lek hypothesis, which employs the mechanisms of lek models to explain colony formation and breeding aggregations in general. The hypothesis predicts that the lek mechanisms also operate in monogamous species that pursue extrapair copulations. Just as less attractive males in promiscuous species aggregate around a hotshot, monogamous males may aggregate around more attractive males to obtain mates, and females may prefer males that defend nesting sites near more attractive males to obtain extrapair copulations from them. If lek mechanisms contribute to colony formation, as suggested by two field studies (Hoi and Hoi-Leitner, 1997; Wagner et al., 1996), then nesting aggregation may be a byproduct of mate choice.

We now illustrate how the processes of breeding habitat selection can also produce aggregations as a byproduct of numerous individuals acting to maximize their fitness. Let's first consider a human example. In the United States and other countries, various regions are periodically discovered to have exceptionally high qualities of life, being free from crime, pollution, and traffic. Such locations are proclaimed by the media to be among the ''10 best places to live.'' As knowledge spreads, individuals imitate the habitat selection choices of their predecessors. Once settlers immigrate to the new area, they do not usually benefit from the arrival of newcomers, who often create the unfavorable conditions they left behind. Thus, it would not be logical to ask how the original inhabitants, now surrounded by a multitude of new neighbors, benefit from living in densely populated areas. The newcomers, likewise, often express the desire to be the last arrivals, indicating that high density settlement can be produced despite net costs to individuals.

Such a simple scenario may often determine animal settlement patterns as well (Boulinier and Danchin, 1997; Danchin et al., 1998; Shields et al., 1988). The habitat selection hypothesis is built on findings in kittiwakes *Rissa tridactyla* that suggest that individuals observe the reproductive success of conspecifics and recruit to the most successful nesting areas in the following year (Danchin et al., 1998). The individuals that occupied the favorable habitat originally often find themselves surrounded by many new neighbors who do not necessarily provide them with any benefits. In fact, no benefits of high density nesting are apparent in kittiwakes, but there is a known cost in the form of increased ectoparasite transmission (Boulinier, 1995; Boulinier and Danchin, 1996; Danchin, 1992). Thus, the habitat selection hypothesis assumes that aggregation is a byproduct of many individuals seeking good breeding habitat by imitating the choices of successful conspecifics. Our point is not to suggest that there are never benefits to breeding in high density, but rather that such benefits are not necessary for colony formation.

If aggregation is a byproduct of commodity selection, then we are asking the wrong question when we search for benefits of high-density breeding. Even when individuals receive net benefits from breeding at high density, it is possible that the benefits accrue only after colonies have been produced as byproducts of mate choice and/or breeding habitat selection. If so, we will never learn how colonies form by correlating breeding density with reproductive success, even when benefits of high-density breeding can be identified. Our aim is not to deny the value of correlational studies, but to underline the importance of distinguishing between patterns and processes.

If the need to select breeding habitat and mates produces aggregation as a byproduct, then why aren't more species colonial? Coloniality occurs in species that exploit food that is ephemeral and patchily distributed, making the food uneconomical to defend. Many other species, however, exploit food that is economically defendable, resulting in large territories that tend to keep breeders separated by substantial distances. We suggest that even noncolonial species have a tendency to aggregate, but are constrained from doing so by the necessity of defending large territories. If this view is correct, then aggregated breeding can be viewed as the ''natural state'' of animals. Although coloniality is implicitly assumed to be produced by strong selective pressures, the opposite view is now also worth considering. Perhaps animals do not space widely because it is typically adaptive to maintain large territories, but rather because they are constrained against aggregating. Supporting this idea is the occurrence of aggregated all-purpose territories in areas where habitat quality is uniform (Ramsay et al., 1999; Wagner, 1997).

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