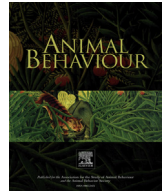


Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Breeding Aggregations

Breeding clusters in birds: ecological selective contexts, mating systems and the role of extrapair fertilizations

Regina H. Macedo ^{a,*}, Jeffrey Podos ^b, Jeff A. Graves ^c, Lilian T. Manica ^d^a Departamento de Zoologia, Universidade de Brasília, DF, Brazil^b Department of Biology, University of Massachusetts, Amherst, MA, U.S.A.^c School of Biology, Harold Mitchell Building, University of St Andrews, St Andrews, Fife, U.K.^d Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil

ARTICLE INFO

Article history:

Received 15 March 2017

Initial acceptance 19 May 2017

Final acceptance 11 December 2017

Available online xxx

MS. number: SI-17-00239R

Keywords:

blue-black grassquit
clusters
coloniality
extrapair fertilization
lek mating system
sexual selection
social monogamy
sociality

Sociality beyond mated pairs, whether in the form of nesting colonies, clustered territories or leks, presents an evolutionary puzzle because densely packed individuals typically incur high fitness costs. One hypothesis to explain clustered distributions is that they overlie clumped distributions of resources. However, numerous studies have shown that resource distributions are often insufficient to explain individuals' settlement decisions, suggesting that clustered breeding distributions are driven by other types of benefits, possibly related to ecological, social and genetic factors. One can ask more specifically whether animals cluster because of some underlying ecological factor, or whether aspects of their reproductive behaviour and mating systems are more influential. Accordingly, evaluating the influence of sexual selection upon the evolution of mating systems can be crucial for understanding the underlying causes of animal aggregations. In this article, we review the behavioural ecology of three types of mating systems where breeding occurs in clusters: colonial, lekking and socially monogamous clustered territorial systems. We highlight sexual selection as a potential explanation for the emergence of aggregations in all three cases. In particular, we discuss the hidden lek hypothesis, which postulates that aggregations in colonial and territorial species can be driven by increased opportunities for extrapair copulations. Finally, we feature our work with the blue-black grassquit, *Volatinia jacarina*, which illustrates the complexity of selective mechanisms that may favour territorial aggregations.

© 2018 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Clustered breeding distributions have been described in very diverse animal groups including insects, spiders, fish, reptiles, dinosaurs, birds, and marine and terrestrial mammals (Podulka, 2004; Rypstra, 1985; Terhune & Brillant, 1996; Treves, 2000; Varricchio et al., 2008). A core explanation for clustered distributions is that they reflect spatially uneven resource distributions, as many individuals in a population choose the same high-quality sites (reviewed in Evans, Votier, & Dall, 2016). However, not all clustered distributions can be explained by concentrated patches of resources. Thus, a comprehensive understanding of breeding clusters requires looking beyond ecological resource distributions to other possible influences (Izkowitz, 1978; Muller, 1998; Stamps, 1988).

The primary goal of our article is to consider some open questions about the evolution of nonresource-based breeding clusters,

especially in light of the possible role of sexual selection and the importance of extrapair copulations. The term breeding clusters here refers to the nonrandom distribution of individuals across the landscape, such that they are close together in a pattern that does not necessarily reflect resource distribution. We discuss clustered breeding in three main contexts, coloniality, lekking and clustered territoriality in socially monogamous species, for which we review associated costs and benefits from an ecological context, while also exploring the possible impact of social and mating pressures. Finally, we consider how these factors might be playing out in a species we have featured in our own work, the blue-black grassquit, *Volatinia jacarina*. Most of our examples in this article are on birds, given our greater familiarity with this group, although we presume that the conceptual context applies more generally to other animal taxa.

In many species that breed in clusters, individual territories are often small, tightly packed and very limited in resources. Aggregated territorial breeding in these cases is known as colonial breeding, and is taxonomically widespread (spiders: reviewed in

* Correspondence: R. H. Macedo, Departamento de Zoologia, IB, Universidade de Brasília, 70910-900, Brasília, DF, Brazil.

E-mail address: rhmacedo@unb.br (R. H. Macedo).

Whitehouse & Lubin, 2005; fish: Van Dongen, Wagner, Moodley, & Schaedelin, 2014; Schaedelin, van Dongen, & Wagner, 2015; birds: Varela, Danchin, & Wagner, 2007; reviewed in Wittenberger & Hunt, 1985; mammals: Pitcher, Harcourt, & Charrier, 2010; Webber et al., 2016). A functional definition of coloniality is when individuals aggregate in breeding densities well above that predicted by the distribution of resource patches (see Evans et al., 2016).

A second category of mating clusters not predicted by resource distributions comprises lekking systems, wherein males usually aggregate within small areas, called arenas, where they display. Females visit and mate with clustered males, after which they depart, build their nests and rear the offspring alone (Höglund & Alatalo, 1995). In lekking systems, females choose partners based on male attributes only, without the influence of direct benefits such as territorial resources or potentially valuable paternal care.

A third main context in which clustering is not directly predicted by resource distributions is in socially monogamous pairs whose territories contain resources other than breeding sites. Resource-based territories are typically much larger than those found among colonial or lekking species. These types of nesting dispersion patterns have been termed 'neighbourhoods' or 'loose' colonies (Lack, 1968). Such clustering of all-purpose territories has not been studied extensively, with most research to date having focused on birds (Almeida & Macedo, 2001; Bohórquez & Stiles, 2002; Greene, Muehler, & Davison, 2014; Tarof, Ratcliffe, Kasumovic, & Boag, 2005; Tiainen, Vickholm, Pakkala, Piironen, & Virolainen, 1983). Nevertheless, even in these systems, resource distribution alone probably cannot fully explain the extent of clustering. In these cases, it has been proposed that sexual selection mechanisms, such as the hidden lek models described below, could encourage the clustered patterns of territories within unsaturated habitats of uniform quality.

Theories describing animal breeding systems, and their diversity across taxa, often build upon basic concepts of sexual selection, since these may explain the variance often observed in reproductive success and reproductive skew (Andersson, 1994; Emlen & Oring, 1977; Owens & Bennet, 1997; Reynolds, 1996). Sexual selection is a process favouring the exaggeration of secondary sexual traits that can increase an animal's chances of leaving descendants in the next generation (Andersson, 1994; Darwin, 1871). According to this theory, individuals in better condition or bearing more extravagant ornaments should gain advantages in the competition for sexual partners. Moreover, sexual selection should be stronger in polygamous than in monogamous species, owing to a higher reproductive skew in the former, in which competition for mates is more intense (Emlen & Oring, 1977). In polygamous systems, only a few individuals are able to attract multiple partners, thus increasing reproductive skew (Andersson, 1994). Multiple mating behaviour should increase individual fitness when polygamy potential is high, that is, when mating partners or limiting resources are economically defensible, mostly when they occur in clumped spatial distributions (Emlen & Oring, 1977). In contrast, social alliances between males and females in monogamy tend to be maintained due to few opportunities for exclusive possession of multiple sexual partners, resulting in reduced variance in reproductive success among males (Emlen & Oring, 1977; Owens & Bennet, 1997) and, in some cases, in females.

Historically, the classification of mating systems has relied upon the study of model species from temperate zones, and accordingly it has been difficult to account for unexpected behaviours in taxa from less well-studied localities such as the tropics (Zuk, 2016; Zuk, Garcia-Gonzalez, Herberstein, & Simmons, 2014). The need for a better classification of animal mating systems was reinforced by the discovery that the sexual mating behaviour of animals does not

necessarily correspond to their social choices (Reynolds, 1996). In fact, conjectures about multiple mating among monogamous birds began in the 1950s, based on observations of extrapair copulations (EPCs; Bray, Kennelly, & Guarino, 1975; Fujioka & Yamagishi, 1981; Gladstone, 1979; von Haartman, 1951). The discovery of widespread EPCs suggested that postcopulatory, prezygotic selection might have a greater impact on avian mating systems evolution than had previously been suspected. In birds, female multiple mating behaviour may trigger sperm competition within the female reproductive tract, resulting in potential female control of paternity (Birkhead & Møller, 1998). In general, however, very few bird studies have been able to test relationships between sexual selection, mating systems and sperm competition, and a clear understanding remains elusive.

BREEDING AGGREGATIONS: ECOLOGICAL AND SEXUAL CORRELATES

Colonial Breeding Systems

Coloniality in birds has evolved independently at least 20 times (Siegel-Causey & Kharitonov, 1990), suggesting that its benefits must be sufficient to override the inherent costs for individuals that breed in colonies. Colonial breeding has multiple costs, such as the potential for increased transmission of pathogens and parasites, elevated competition for resources including food and mates, and higher mortality of young due to cannibalism and infanticide (Brown & Bomberger Brown, 1996; Møller, 1987). Some of the main driving forces for colonial nesting are ecological in nature. Absence of specific predators, resource restriction and prey aggregation may lead animals to establish colonies passively, where individuals do not necessarily cooperate or even interact with conspecifics, but instead merely tolerate them.

A multispecies comparison based on observational data suggests that copulations with multiple partners occur more frequently in colonial birds than in closely related solitary species (Møller & Birkhead, 1993; but see Griffith, Owens, & Thuman, 2002). Interestingly, the higher incidence of cuckoldry associated with clustered individuals can be considered both a cost, for cuckolded males (Alexander, 1974; Birkhead, 1979; Birkhead, Atkin, & Møller, 1987; Gladstone, 1979), and a benefit, for females and males that achieve extrapair matings (Bain, Hall, & Mulder, 2014).

The evolution of colonial nesting has been examined using two main approaches. One is the traditional ecological framework, which entails a functional assessment of costs and benefits to group living (Alexander, 1974; Wittenberger & Hunt, 1985). A second approach focuses on commodity selection, and builds on the assumption that individuals choose their breeding sites based upon the availability of commodities such as habitat and mates. This approach, which considers proximate mechanisms of habitat choice (Danchin & Wagner, 1997), posits that animals aggregate incidentally because they make parallel choices regarding preferred habitats. For example, in choosing a habitat, individuals can copy the choices of other individuals that are breeding successfully (Boulinier & Danchin, 1997; Danchin, Boulinier, & Massot, 1998).

Considering first the traditional approach, the ecological benefits that may favour the evolution of coloniality are numerous. A geometrical model of foraging proposes that coloniality may provide members with shorter distances to foraging areas (Horn, 1968). Other possible benefits include high-quality but limited nesting sites (Lack, 1968; Wittenberger & Hunt, 1985), protection from predators due to a location's inaccessibility (Buckley & Buckley, 1980), decreased risks of predation due to the dilution effect and increased opportunities for vigilance (Alexander, 1974;

متن کامل مقاله

دریافت فوری ←

ISIArticles

مرجع مقالات تخصصی ایران

- ✓ امکان دانلود نسخه تمام متن مقالات انگلیسی
- ✓ امکان دانلود نسخه ترجمه شده مقالات
- ✓ پذیرش سفارش ترجمه تخصصی
- ✓ امکان جستجو در آرشیو جامعی از صدها موضوع و هزاران مقاله
- ✓ امکان دانلود رایگان ۲ صفحه اول هر مقاله
- ✓ امکان پرداخت اینترنتی با کلیه کارت های عضو شتاب
- ✓ دانلود فوری مقاله پس از پرداخت آنلاین
- ✓ پشتیبانی کامل خرید با بهره مندی از سیستم هوشمند رهگیری سفارشات