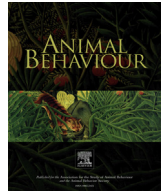




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Special Issue: Breeding Aggregations

Friend or foe? The dynamics of social life



Natural history observations of complex social interactions in many animal species have led to decades of research concerning the origins and functionality of animal groupings. The settings of such groups vary greatly, ranging from animals in close proximity during foraging or hunting to grouped individuals exhibiting intricate courtship displays, and have led to a diversity of explanations for aggregation behaviour. Darwin (1859) discussed how such social groupings might emerge, along with their possible benefits and costs, in the context of sterile insect castes. Many other considerations about sociality have followed over the years, yet it is remarkably difficult to find a formal definition of sociality or social behaviour in biology or animal behaviour textbooks. The assumption seems to be that social behaviour is so obvious that it needs no definition. Perhaps, as social animals ourselves, we overlook the large variability encompassed in the concept. However, it is quite easy to observe a clear distinction among animals, that some lead a solitary life, while others generally are found in groups. Here, we will use the definition of a social group as ‘a collection of individuals that actively cluster together, exist in close proximity in both space and time, and engage in behavioral interaction; a social group also is a discrete unit that is distinct from other such groups’ (Earley & Dugatkin, 2010, p. 285). However, for our purposes, we interpret this definition perhaps more broadly than its original intent, including animals whose territories are grouped together. We interpret such occupation of the habitat to be an active choice, giving rise to nonrandom patterns of clustering that result in many types of social interactions, including competitive exchanges as well as cooperative behaviours.

Unifying explanations for animal aggregations were lacking until Wynne-Edwards (1962) published an explanation for social behaviour that hinged on group selection. This work unintentionally engendered focused critiques that eventually led to greater understanding about the biological foundations of social evolution (Hamilton, 1963, 1964; Trivers, 1971, 1972; Williams, 1966, reviewed in Alexander, 1974). The theoretical framework proposed in these classical publications spurred much empirical work attempting to fill in the numerous gaps in knowledge about almost all social animals.

The goal of this Special Issue is to update this scenario. Recent studies have expanded explanations for the evolution and maintenance of sociality in a wide array of animals. If there is one general principle, it is that there is no single, all-encompassing explanation underlying social evolution. Most broadly, a critical perspective about sociality involves the assessment of the costs and benefits for individual group members. The scale tilts in one direction or the other, depending on how great the benefits and how dire the costs. Thus, one finds that social groups vary greatly. They may

include unrelated or related individuals, members of only one sex, a dominant male with a harem of females, or even groups that contain individuals of different species.

In the contributions prepared for this Special Issue, authors take a closer look at aggregations that occur in the specific context of breeding. However, the broader context of sociality involves two central issues that we briefly discuss below as a general introduction to the common theme of breeding aggregations. First is the question of costs versus benefits as major selective forces that drive animals into groups and maintain group membership. The second issue is that of behaviours and mechanisms that evolve once animals are clustered, which are difficult to distinguish from benefits derived from sociality. Within this category are many specific adaptations and specialized behaviours, such as helping activities or alarm calling, among others, that make social living an attractive option.

Costs of Sociality

A commonly held starting point for thinking about the biological basis of sociality is that membership in groups generates benefits that outweigh the costs for all involved individuals. An alternative explanation is that sociality per se may generate no benefits, but ecological constraints make solitary living either a less viable and therefore costlier option, or completely unfeasible. Consequently, some species exhibit facultative sociality, such that specific individuals may be able to lead a solitary life, depending on their age, sex or ecological conditions. Group size can have a significant and multifaceted influence on many social parameters. For example, group size is associated with stress and social conflict among group members (Maestriperi & Georgiev, 2016; Pride, 2005; Snaith, Chapman, Rothman, & Wasserman, 2008), disease transmission (Côté & Poulin, 1995; Davies, Ayres, Dye, & Deane, 1991; Dobson & Hudson, 1986; Loehle, 1995; Nunn & Heymann, 2005; Rifkin, Nunn, & Garamszegi, 2012), and general patterns of breeding and behaviour (Griffiths & Magurran, 1997; Nunn, Thrall, Bartz, Dasgupta, & Boesch, 2009). Despite these different perspectives, the costs of living socially are more intuitively obvious than are the benefits.

Generally, it is assumed that larger groups have higher levels of competition and therefore more social conflict (Alexander, 1974). Empirical studies, however, have shown that the relation between group size and social conflict is neither linear nor simple (Amsalem & Hefetz, 2011; Clutton-Brock, Hodge, & Flower, 2008). This relationship was modelled by Shen, Akçay, and Rubenstein (2014) to explore how different ecological and social conditions could influence the degree of conflict within groups. The model suggests that

when groups form primarily because of the benefits of sociality, there should be a positive relationship between social conflict and group size. On the other hand, when groups form as a means to access group-defended resources, there is no positive relation between group size and conflict. Thus, the model suggests that identification of the primary reason for group formation may yield important clues relative to degree of social conflict.

The association between group size and social conflict has been studied across many different taxa. Consider, for example, the behaviours exhibited by the communally breeding birds known as anis, which exhibit both cooperative (e.g. nest building, alarm calling) and competitive (e.g. egg ejection, infanticide) behaviours (Davis, 1942). For these species the communal clutch size and the number of ejected eggs increase with group size (Riehl, 2011; reviewed in Macedo, Cariello, Graves, & Schwabl, 2004; Vehrencamp & Quinn, 2004). Another example is a study focusing on social behaviour of folivorous red colobus monkeys, *Procolobus rufomitratu*s, which concluded that differences in behaviour were best explained by variation in group size, with the latter having a higher impact on behaviour than environmental factors such as rainfall or food availability. In species that establish dominance hierarchies and that exhibit very sophisticated and complex patterns of social behaviours, as do many primates, the cost–benefit ratio of group life may differ for group members (Maestripieri & Georgiev, 2016). In primate societies, benefits generally arise from protection against predators as well as from the cooperative acquisition of food (Wrangham, 1980; van Schaik, 1983). Despite such benefits, undeniable costs generated by conflicts of interest have been documented, including increased competition for food and mating opportunities. Thus, the cost–benefit equation that can drive the evolution of sociality usually varies so that individual members accrue different benefits and are subjected to varying degrees of the costs imposed by group membership. The highest cost that can be imposed upon the lowest-ranking individuals may well determine group cohesion and fate.

Parasitism is frequently cited as one of the most serious costs of sociality, imposing a limit on group size. A host of studies suggests that dense aggregations of individuals increase the transmission of parasites, often changing the functionality of entire ecosystems (reviewed in Côté & Poulin, 1995; Dobson & Hudson, 1986; Rifkin et al., 2012). Mathematical models developed to explore quantitative predictions about the dynamics of disease transmission indicate that the rate of new infections is density dependent and nonlinear, signifying that a parasite can only be maintained in the host population if the host's density is above a certain threshold value. Despite the number of reports indicating a positive association between group size and rates of parasitism, researchers have been busy exploring the factors that may account for variation in infection levels and diversity of parasites (reviewed in Kappeler, Cremer, & Nunn, 2015). One expectation is that larger groups should be associated with higher levels of infection by parasites that depend on social transmission, whereas for mobile parasites, such as biting flies, such an association may not exist (Côté & Poulin, 1995). Echoing the overall result that larger groups result in higher levels of disease transmission, Nunn, Jordán, McCabe, Verdolin, and Fewell (2015) reported that social substructuring – effectively, the existence of smaller social groups within larger ones – mitigates the negative effects of large groups on disease and parasite transmission. Factors beyond group size, including social class and territoriality, have been found to be important in determining levels of parasite infection risk for some taxa (Ezenwa, 2004).

It is plausible that social evolution has also produced, at least in some cases, an increased capacity to resist parasites and diseases through social behaviours that reduce pathogen transmission.

Social behavioural mechanisms complement the numerous behaviours essential in reducing the risk of parasitism and disease, such as feather preening, fur and wound licking, dust or mud bathing, and cleaning of nests or dens, among others (reviewed in Loehle, 1995). Social adaptations might include social avoidance of individuals that exhibit external signs of disease, avoidance of sick individuals in the mate choice and monogamous long-term relations that prevent sexually transmitted diseases (reviewed in Loehle, 1995).

Benefits of Sociality

Alexander's (1974, p. 326) pivotal explanation for social evolution upheld that '... groups form and persist because all of the individuals involved somehow gain genetically.' He then went on to classify different types of groupings, emphasizing genetic relatedness among group members. Alexander's coherent discussion suggests that all benefits of grouping fall into two selective contexts, which involve either decreased predation (e.g. through predator mobbing) or better resource exploitation (e.g. defensive group behaviour to monopolize resources).

Protection from predators is a powerful agent for the evolution of sociality. Empirical support for this idea has accumulated for many diverse taxa, ranging from insects and spiders to fish, birds and mammals (Blumstein, Daniel, & Bryant, 2001; Blumstein, Daniel, & Evans, 2001; Blumstein, Daniel, & McLean, 2001; Bono & Crespi, 2006; Coster-Longmann et al., 2002; Hass & Valenzuela, 2002; Hess, Fischer, & Taborsky, 2016; McGowan & Woolfenden, 1989; Uetz & Hieber, 1994; Waterman, 1997; White & Cameron, 2009). For example, the cooperative antipredator behaviours of species in the mongoose family (Herpestidae) include shared vigilance, coordinated sentinel systems, predator mobbing and dilution effects (Graw & Manser, 2007; Manser, 1999; Schneider & Kappeler, 2016).

The second major context where group living could be adaptive, as suggested by Alexander (1974), is that of acquiring resources. This could be further subdivided into situations where groups can (1) forage more efficiently, for example by cooperatively capturing large or difficult prey, or (2) obtain information about food sources. Social hunting occurs in a broad array of taxa, from insects and spiders to birds and terrestrial and aquatic mammals (Baird & Dill, 1996; Busse, 1978; Ford et al., 2005; Guinet, Barrett-Lennard, & Loyer, 2000; Götmark, Winkler, & Andersson, 1986; Hector, 1986; Packer, 1986; Ward & Enders, 1985). Despite the advantages gained by individuals in this context, it remains unclear whether sociality in these cases evolved because of the advantages gained through cooperative foraging/hunting. Rather, it is possible that the latter might have evolved as an adaptation to sociality. Theoretical considerations suggest that sociality based upon cooperative hunting behaviour can only evolve when the per capita energetic intake of the group exceeds what would be possible with solitary hunting (Clark & Mangel, 1986; Sibly, 1983).

Alexander suggested that beyond the contexts of predator avoidance and resource exploitation, grouped individuals are forced into dense aggregations because of resource restrictions and their localized distribution in the environment. Although these arguments are still relevant to any discussion of sociality, recent empirical studies suggest additional selective settings that favour social life. Within the context of social foraging, a somewhat neglected subject involves the use of conspecific group members as sources of information about resources. This idea is rooted in the observation that colonial birds typically consume prey available in patches that are spatially and temporally unpredictable. Thus, they could benefit from acquiring information about the location of food patches before departing on foraging trips. Early accounts strongly support the idea that communal roosts or colonies could

function as information centres (Ward, 1965). While some studies confirmed that social information transfer occurred for some species (Brown, 1986; Burger, 1997; Thiebault et al., 2014; Waltz, 1987), other studies refuted the hypothesis of an information centre function for colonies or roosts (Davoren, Montevecchi, & Anderson, 2003; Loman & Tamm, 1980; Mariette & Griffith, 2013; Mock, Lamey, & Thompson, 1988). Some of the assumptions of the original information centre hypothesis have been an obstacle to its applicability for a broader number of species. One of the more recent discussions of this hypothesis suggests dropping the assumption that the information transfer is actively made, and instead considers that social information most likely is conveyed inadvertently (Bijleveld, Egas, van Gils, & Piersma, 2010). The idea that involuntary information transfer takes place within social groups gained traction, and concepts known as 'eavesdropping' and 'public information' have become more important in the discussion of social evolution, as pointed out in recent reviews (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Danchin, Giraldeau, Valone, & Wagner, 2004).

Benefits of Sociality in a Breeding Context

Sociality may generate benefits that enhance survival and reproductive success for all group members, including offspring. However, it is hard to discriminate between benefits such as predator dilution effects, thermoregulation, enhanced social foraging and more restricted group effects directed toward the production and care of offspring. In this latter category are such behaviours as babysitting, brood guarding, adoption and nonoffspring nursing or feeding (Russell, 2004). Collectively, such behaviours can be included within the context of cooperative breeding, a phenomenon originally described by Skutch (1935) in which bird pairs are joined by helpers-at-the-nest to rear their young. The paradox of helping behaviour is that it encompasses individual sacrifice in terms of risk, energy or individual fitness costs. This puzzle, which was discussed by Darwin (1859), remained a biological puzzle for over a century, and was partially resolved by inclusive fitness and kin theory (Hamilton, 1964). The broader phenomenon of cooperative reproduction also includes phenomena other than 'helping at the nest'. For example, males of a wide range of species may form reproductive coalitions to attract, defend or coerce mates (Díaz-Muñoz, DuVal, Krakauer, & Lacey, 2014), and these coalitions are also influenced by the forces of natural, sexual and kin selection on group behaviour. Complex social interactions, including cooperation, can play an important role in the formation and maintenance of breeding aggregations.

In an array of vertebrate taxa, genetic relatedness yields inclusive fitness benefits and appears to be the most important driving force for the evolution of cooperative breeding (Koenig & Dickinson, 2016). However, not all cooperatively breeding groups are composed of genetically related individuals, and helpers may be completely unrelated to the breeding adults and offspring they are helping. Intriguing cooperative behaviours devoid of a kinship link exist in many species or cases where group members have low levels of relatedness but still exhibit cooperative behaviours (Blanchard, 2000; DuVal, 2007; Macedo, 2016; Riehl, 2011; Shen, Yuan, & Kiu, 2016).

Within the context of sociality and reproduction, it is often the case that animals form aggregations during their breeding periods, with or without cooperative behaviours. They may interact socially, especially in coordinated defensive behaviours or to acquire information, but the factors leading to such agglomerations may vary and remain unclear. These types of breeding aggregations include colonial animals and clustered territories of socially monogamous birds, as well as lekking species. The link between sociality and

breeding can include many contributing factors, some of which are detailed above, such as kinship or predator deterrence. However, many other specific selective forces may be at play. In this Special Issue, the contributions of different authors highlight the causes and consequences associated with the clustering of animals during breeding. The data and results compiled in these studies, as outlined below, emphasize the complexity of behavioural and ecological correlates of breeding aggregations in some biological systems.

Overview of This Special Issue

Animal aggregations often have direct effects on access to and interactions with potential mates. This perspective complements the historical focus on the role of aggregations in processes related to survival, summarized above. Aggregations, however, also directly affect access to and interactions with potential mates. Macedo, Podos, Graves, and Manica (2018) review the varied influence of sexual selection on breeding aggregations in colonial, lekking and socially monogamous species. They specifically highlight the contributions of the hidden lek hypothesis in understanding the role of mating opportunities in selecting for – or against – breeding aggregations, using the blueblack grassquit, *Volatinia jacarina*, as a model for testing the hypothesis.

New insights frequently result from considering new model systems. Pruitt and Avilés (2018) consider the types of adaptations that may result from group living, highlighting social spiders as a thought-provoking 'biological novelty item' – an oddity in a taxon better known for conspecific aggression. This model may therefore offer new insights into the evolution of social aggregations.

Living in groups requires effective communication. Webster, Ligon, and Leighton (2018) investigate the role of social costs in maintaining honest signals of quality or motivation in interactions with mates and rivals. Instead of receiver-independent costs to producing a particular signal, such as the time or energy required to create the signal, the authors focus on receiver-dependent costs that vary with social context. They review the evidence that social interactions affect signal production, and underscore the need for more research on social costs of signalling interactions that may be important for understanding the balance of costs and benefits that underlie social aggregations.

When animals breed in groups, group sizes may vary widely and puzzlingly, and the fitness effects of such variation are often unclear. Brockmann, St Mary, and Ponciano (2018) explore variation in breeding aggregations of horseshoe crabs, in which a breeding female and an attached male may be joined by a highly variable number of satellite males. The authors demonstrate that although operational sex ratio and pair density explain some variation in the distribution of aggregation types observed, these patterns are generated by random joining of a breeding group by satellites. This paper offers a compelling and flexible technique to investigate null hypotheses about distributions within breeding aggregations. Likewise, Solomon and Keane (2018) investigate the role of breeding group size on success in wild prairie voles, *Microtus ochrogaster*. This species is best known for its monogamous breeding pairs, but several females may breed in the same burrow system. The authors' field studies suggest that, contrary to previous reports, there is not a clear reproductive benefit to mid-sized breeding groups. Instead, time that females were present in the monitored area was the best predictor of reproductive success.

The costs and benefits for long-lived animals that breed in aggregations may depend partly on age or experience. Both Strong, Sherman, and Riehl (2018) and DuVal, Vanderbilt, and M'Gonigle (2018) identify tenure in a breeding location as an important factor

modifying the outcomes of interactions in breeding aggregations, albeit in very different breeding systems. Strong et al. (2018) report that in greater anis, *Crotophaga major*, larger groups are not more successful, thus rejecting size of the breeding group as an important predictor of success. Instead, they show that individual fitness correlates with tenure as a breeder. DuVal et al. (2018) investigate male performance on an exploded lek of lance-tailed manakins, *Chiroxiphia lanceolata*, and find that alpha males that are closer to other alphas are visited by more females, but that the fitness effects of this increased traffic depend on a male's years of tenure in the alpha role. Only the most experienced individuals have increased siring success when they are in close proximity to other alphas.

In summary, the papers in this Special Issue focus on current questions relevant to a better understanding of both social and ecological factors that promote animal breeding aggregations. We hope the questions raised in these studies can be applied to advance new concepts within the scope of social evolution theory. We thank the authors in this Special Issue for their enthusiastic contributions.

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Regina H. Macedo, Emily H. DuVal
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