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## **The dynamics of social behaviour — the importance of dispersal and the environment**

Social behaviour garners broad interest: biologists, social scientists, psychologists and economists all incorporate a consideration of social behaviour in their studies. This breadth of interest is unsurprising, as the vast majority of animals live in social environments, and their lives are affected by the presence and activity of others around them. Social behaviour takes diverse and fascinating forms in a wide variety of taxa. Individuals spend time interacting with members of their own, or other, species, they attract mates, care for offspring and group together for hunting or safety, and migrate from one site to another (Wilson, 1975; Dugatkin, 1997). There are, however, differences between individuals, populations and species in the extent of the amount of social interactions and expression of social behaviour. These differences are explained in the context of evolutionary theory, based on the idea that individuals are selected for their ability to efficiently translate resources into fitness (survival and production of young), maximizing their genetic contribution to future generations (Fisher, 1930; Wright, 1932; Hamilton, 1964; Maynard Smith, 1964). Individuals with the most suitable genetic material to perform under prevailing conditions will, thus, contribute to future generations more than others with inferior genotypes. This would appear to lead to a world dominated by selfish behaviour. As a consequence, the evolution of behaviour, including social behavior, should be driven by relative costs and benefits (e.g., Maynard Smith, 1977; Clutton-Brock, 1991). For example, the amount of paternal care to offspring may be adjusted in line with confidence of genetic parentage (Westneat & Sherman, 1993), or non-breeding adults may cooperate with their relatives to enhance the reproductive output of their kin (e.g., Russell & Hatchwell, 2001; Richardson et al., 2003). Given that social behaviour is often costly and the amount of social interactions underlies almost all of the processes that result in fitness variation, the understanding of social evolution is challenging. Behavioural ecologists traditionally investigated the evolution of social behaviour by studying adaptation and the effects

of behaviour on survival and reproductive success. However, the combined roles of the social environment in which individuals live (e.g., the availability, distribution and competition for resources such as food and mates) and the amount of social interactions between individuals on the expression of individual behaviours (propagating survival and reproduction) have rarely been considered.

In the context of social behaviour, animals also create selection on themselves by interacting with each other. These social interactions provide a functional link between individual and population processes. The survival, reproduction and distribution by active movements of animals across environments are often the outcome of social interactions, where population density affects the evolution and expression of individual behaviour, for example by influencing the frequency of encounters and the intensity of competition between individuals. However, the environment varies in the availability and suitability of habitats for animals to settle in, which in turn often affect social interactions and with that survival and reproductive success of breeding populations in territorial animals. This highlights the mutual feedback mechanisms between ecology and sociality. Extensive theoretical and empirical research on behaviour has shown that population size and density may influence a range of ecological and life-history variables, including competition for food and territories (e.g., Kokko et al., 2004; Alonzo & Sheldon, 2010), and for mates (Owens, 2002; Forsgren et al., 2004; Kokko & Rankin, 2006; McGraw et al., 2010). The idea that environmental conditions, and habitat saturation in particular, limits breeding populations in territorial animals has a long history with its roots in population ecology. A process describing how habitats become saturated in crowded populations was termed the “buffer effect” by Kluver & Tinbergen (1953). Their model was designed to explain the regulation of population numbers in a habitat of varying quality. As a basic premise it assumes that habitats are filled in order of quality. First optimal habitat becomes filled, and then suboptimal habitat, until there is no suitable habitat available for reproduction (Brown, 1969). As habitats of better quality are gradually filled up, remaining vacant space eventually becomes of such poor quality that would-be breeders deem it unsuitable as breeding habitat. The fraction of the population without a territory adopts the role of floaters until a breeding vacancy becomes available. Furthermore, an increase in population density usually has negative feedback effects on

reproduction and survival through conflicts over resources. As density increases, the abundance of food decreases and breeding vacancies become rare and individuals may choose to either disperse to suitable feeding and breeding sites or remain and face competition over resources. The “buffer effect” caused by environmental heterogeneity in the suitability and availability of habitats for animals to settle in, often creates spatial variation in density of individuals. This is further augmented by temporal variation in density, due to variation over the course of reproductive and annual cycles and to longer-period variation (e.g., climatic effects on population size, population cycles in prey, changes of environments; see Turchin, 2005). Hence population density is variable at the short-term and the long-term level. This variability in density should have an effect on the amount of social interactions, which in turn affects individual behaviours causing them to vary among individuals within the same population. Inferences about the effect of density on behaviours will depend on the temporal and spatial scale at which density is measured and, therefore, varies among individuals within the same population. Yet until now, we have paid little attention to the importance of an individual’s immediate social environment (interaction with other individuals) on the plasticity and adaptability of an individual’s decisions (see also Bergmüller & Taborsky, 2010). In this Special Issue we aim to highlight the interplay between dispersal and sociality in a spatially structured environment in relation to density-dependent and density-independent processes and population dynamics. We take a cross disciplinary approach using original research covering a range of taxonomic groups (insects, fish and birds).

### **Interactions between density, dispersal and social behaviour**

Population size and density affect the frequency of individual encounters, influencing mating opportunities and breeding systems. One factor through which population size and density affects individual reproductive strategies is through changes in individual dispersal strategies. For example, it has been shown that as local breeding density increases, natal dispersal distance — dispersal distance from birth place to the place of reproduction — decreased (Forero et al., 2002; Eikenaar et al., 2008). In contrast, Richardson et al.

(2010) found no effect of population density on natal dispersal in the endangered hihi (stitchbird, *Notiomystis cincta*) in New Zealand. After a reintroduction to Tiritiri Matangi Island in 1995, the population increased considerably, but natal dispersal distances did not change. However, it was shown that there was a strong negative relationship between cohort size and male dispersal distances. It is hypothesized that in the early stages of population establishment when densities are low males are able to disperse and secure the higher quality territories within the confines of the island which are still unoccupied after population establishment, but as population density increases, dispersal decisions become increasingly constrained by territory availability, and possibly variation in mating strategies. In later years, the sex ratio was a more important influence on natal dispersal by females, with females dispersing further when the population was more male-biased.

The effect of density on individuals is generally mediated through social interactions, which will also vary spatially and temporally. For example, males in a high density population will have the opportunity to find one or more females, whereas in a low density population it may be difficult to find a partner or multiple females in the appropriate reproductive phase. As such, population density and with that the number of potential mates may influence the mating system and parental care strategies. Yet individuals are not likely to experience the same population density, either because they come from different parts of an organism's range or from different habitats in which the local density varies. Hoi et al. (2010) provided evidence for an influence of local breeding density on the rate of local conspecific brood parasitism in female bearded tits (*Panurus biarmicus*). Local conspecific brood parasitism involves the laying of eggs in nests of conspecific hosts, which are left under parental care of the host parent. They found that solitary female breeders suffered less from conspecific brood parasitism than females breeding in colonies. However, the observed increase in conspecific brood parasitism could well be a by-product of a density effect such as genetic relatedness among individuals. With an increase in density the individuals may be more related to each other, and as such host individuals will be more likely to tolerate related conspecific offspring. This was not the case in bearded tits, because only half of all egg dumping attempts was successful, and parasitic hatchlings develop less well than their non-parasitic brood mates. Contradicting this prediction, females breeding in higher density do not have better anti-parasite strategies, such as removing the parasitic egg from the clutch.

Population differences in density, which have an influence on availability of breeding partners, may also influence the resolution of sexual conflict (Kokko & Rankin, 2006; Rankin, 2007). Sexual conflict occurs when males and females have separate and conflicting routes to increase fitness. The effect of population density on sexual conflict has rarely been studied (Székely et al., 1999; Kosztolányi et al., 2006). Van Dijk et al. (2010) investigated the influence of breeding density on the resolution of sexual conflict over parental care in the penduline tit (*Remiz pendulinus*). Penduline tits exhibit three patterns of parental care: female-only care, male-only care, and no care, and there is a major cost involved with bi-parental desertion resulting in clutch loss (Persson & Öhrström, 1989). Each sex may mate with several partners over a breeding season. Given that each of the parents should prefer its mate to face the costs of parental care, a sexual conflict over care arises. Van Dijk et al. (2010) investigated several populations across Europe and demonstrated that breeding density has an influence on mating opportunities for males and females. However, despite these substantial differences, there was no difference in the frequencies of parental care patterns associated with different densities. The overall breeding system is consistent across populations including the striking frequency of biparental desertion (30–40% in all populations). These results are in contrast with other studies showing that mating opportunities play an important role in determining differences in the type of parental care (Davies, 1992; Balshine-Earn & Earn, 1998; Székely et al., 1999; Pilastro et al., 2001; Owens, 2002) or in the outcome of sexual conflict over care (e.g., McNamara et al., 2000; Pilastro et al., 2001; Houston et al., 2005). It seems that parental care patterns in penduline tits are fixed and this may suggest a genetic constraint that is not responding to selection on adaptive adjustment to local conditions, i.e., density dependent influence on desertion behaviour. Local adaptations in this species may not occur because the species exhibits a low site-fidelity between seasons (van Dijk et al., 2008) and may even disperse over a long distance during the breeding season (Franz et al., 1987), which may lead to an increased gene flow and possibly annihilate local selection pressures (Garant et al., 2005; Price, 2008). As such the relationship between ecological variables, breeding density and parental care is likely more complex than a mere association mediated through mating opportunities (Leisler et al., 2002; Kosztolányi et al., 2006; Eldegard & Sonnerud, 2009). It has been assumed that the differences in behaviours and strategies employed by individuals to maximize their inclusive fitness

are largely because of behaviourally plastic responses to the environment (Sih et al., 2004; Pennisi, 2005). However, the penduline tit study showed an absence of behavioural plasticity despite consistent differences in environmental situations. Other studies have demonstrated consistent differences in the extent of behaviour towards the same environmental stimuli between individuals belonging to the same or different populations (Taborsky, 1994; Gross, 1996; Brockmann, 2001; Dingemanse et al., 2003; Drent et al., 2003).

In addition to parental care behaviour, dispersal patterns and habitat settlement decisions in relation to varied ecological environments can also be influenced by inflexibility of gene expression and/or by early parental effects (Brown & Brown, 2000; Pasinelli et al., 2004; Hoover & Hauber, 2007). Richardson et al. (2010) found in the hihi, that the individual's mother influenced natal dispersal distance when accounting for other variables, including the nest box hatched in. Dispersal distances were similar for individuals cared for by the same females, suggesting that genetic or maternal effects may contribute to individual dispersal distances. However, it could well be that maternal effects on natal dispersal decisions are confounded by local environmental effects, because breeding females show strong breeding site fidelity during their breeding tenure. The effects of maternal and environmental effects on dispersal should be investigated by experimentation, for example through cross-fostering hatchlings between nest-boxes in different environments to tease out genetic, maternal and environmental effects on dispersal.

### **Interactions between environmental heterogeneity, dispersal and social behaviour**

Spatial or temporal variation in local environmental factors, such as the distribution of predators and food over a population, also may have feedback effects on individual behavioural traits. In fish, for example, the presence of predators affects the formation of shoals (Krause & Ruxton, 2002). Individuals in larger shoals experience lowered predation risk than individuals in smaller shoals owing to confusion and dilution effects. According to the confusion effect, predators have difficulty identifying and capturing a single individual fish within a homogenous group (Magurran & Pitcher, 1987). The larger the shoal, the smaller is the chance that an individual is being killed

during an attack. This defence mechanism will depend on fish choosing to associate with large shoals. Dougherty et al. (2010) have demonstrated an effect of shoal size on grouping behaviour in fish. Juveniles of three fish species reared in isolation from birth and without any prior experience with other fish, were all capable of discriminating between shoals of different sizes, and chose to join large shoals over small shoals. These results demonstrate innate ability in juveniles to choose large shoals over small shoals. However, shoal size preference was also influenced by experience. Individuals raised from birth in groups of three, did not show a preference for a smaller or larger shoal. It is possible that these fish, exposed to the pressures of intra-specific competition, simply chose smaller, less competitive shoals that enabled increased food uptake.

A change in behaviour also may occur when populations do not change in size or density. Eikenaar et al. (2010) demonstrated in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*) that both sex-specific natal dispersal and helping behaviour are biased in relation to a change in the distribution of insect food resources (territory quality) and not to changes in population size or density. The island warbler population has remained stable in size and density from 1985 onwards. In this saturated population, most male and female offspring remain in the natal territory and disperse only when they are able to claim a vacant dominant breeder position (Eikenaar et al., 2009). At first, from 1985 onwards, the population had a very steep territory quality gradient and delaying dispersal was a better fitness option than dispersal for offspring born on high quality territories while dispersal was the better fitness option for offspring born on low quality territory (Komdeur, 1992). At that time there was male-biased dispersal and female-biased helping because females were usually born on higher quality territories than males (Komdeur et al., 1997), which delayed dispersal for a longer period than males and more often became helpers. Eikenaar et al. (2010) show that over the last decades the territory quality gradient across the population had gradually flattened due to restoration of the island vegetation and its associated insect food, which resulted in a decline and eventually in an absence of sex-biased dispersal and helping. Fewer females delayed dispersal from high quality territories and fewer males dispersed from poor quality territories and more males became helpers. Numerous studies have reported sex-biased natal dispersal, which seems to suggest that a sex bias in delayed natal dispersal is a species or population constant (Greenwood,

1980; Greenwood & Harvey, 1982; Clarke et al., 1997). However, the findings in the Seychelles warbler strengthen the view that a sex bias in natal dispersal and helping can be a highly plastic behavioural response to local ecological circumstances. These findings are in contrast to the absence of changes in sex-specific care strategies in penduline tits (van Dijk et al., 2010). The temporal change in sex-specific dispersal may lead to changes in population structure and in the frequency of individual encounters of the same sex and different sexes and, thus, the potential for mating opportunities, and competitive and cooperative interactions between individuals.

### **Ecological heterogeneity and competitive interactions between individuals**

While the causes for dispersal are likely diverse and situation-dependent, inbreeding avoidance (mating with genetically dissimilar partners) plays a central role in the evolution of natal dispersal (Perrin & Goudet, 2001). The absence of substantial dispersal or sex-biased dispersal may lead to competitive interactions of the non-dispersing individuals and non-dispersing sex, respectively. This may affect both local population density and patterns of relatedness among individuals. In case of lowered natal dispersal and high nest site fidelity the chance of inbreeding (mating with a close relative) increases, which may result in a cost, such as reduced hatching and offspring survival (Akçay & Roughgarden, 2007). To circumvent the costs of inbreeding, extra-pair copulation behaviour might serve as a mechanism to avoid the costs of inbreeding. The costs of inbreeding and, thus, the adaptive value of seeking genetically dissimilar mates have been well-documented (e.g., Charlesworth & Charlesworth, 1987; Keller & Waller, 2002). Huyvaert & Parker (2010) showed in the waved albatross (*Phoebastria irrorata*), mostly confined to one small island in the Galápagos, that, despite inbreeding costs in the form of reduced hatching success, there was no positive relationship between genetic similarity of social mates and extra-pair occurrence. Their finding refutes the avoidance of inbreeding costs. Moreover, cuckolded males were more genetically similar to randomly chosen breeding males than to the genetic sires of their extra-pair offspring, suggesting that the overall genetic relatedness (genetic similarity) in the breeding colony is higher than the genetic similarity of females and their social mates. This finding indicates that female albatrosses seem to choose mates to maximize genetic complementarity instead

of strictly avoiding extreme inbreeding or outbreeding. Extreme outbreeding may have detrimental effects on local adaptations because it offsets genetic depression resulting in lower offspring fitness (Pusey & Wolf, 1996; Kokko & Ots, 2006). The effects of genetic complementarity on offspring fitness need further study in the albatrosses.

A spatial model by Rankin (2007) suggests that the density of conspecifics strongly influences the cost benefit trade-off maintaining competitive traits in males. As population densities decrease and local competition is reduced, the relative costs of expressing competitive traits outweigh the benefits conferred to the individual. Therefore, if densities vary amongst populations, it is likely that the magnitude of competitive male traits will vary as well. The balance of these conflicting dispersal patterns creates an intriguing form of stabilizing selection on male traits, such as the degree of aggression. Unlike negative frequency dependent selection within groups, stabilizing selection is produced by the balance of opposing selection at alternate levels. Directional selection favouring aggression at the local scale is balanced by directional selection favouring non-aggression at the larger scale of groups, maintaining individual differences in aggression in the total population (Eldakar et al., 2009a). Males frequently diminish the long-term reproductive success of females in an effort to outcompete rivals in the short-term (Chapman et al., 2003). Selection favoring individual self-interest in the form of the overexploitation of a shared resource, such as mates or food, can lead to the exhaustion of the resource and detrimental consequences for the group ('tragedy of the commons'; Hardin, 1968; Rankin et al., 2007). In regard to sexual conflict, over-exploitation in the form of the excessive harassment of females by aggressive males can also yield similar consequences resulting in decreased female fecundity as well as increased female mortality (e.g., Bauer et al., 2005; Le Galliard et al., 2005; Rankin & Kokko, 2006). As such the presence of aggressive males in isolated populations could have repercussions for future reproduction. Eldakar et al. (2010) investigated the effect of local population structures — frequency of aggressive male phenotypes — on behavioural differences and subsequent phenotype distribution in natural populations of water striders (*Aquarius remigis*). In males the degree of aggressiveness and dispersal tendency are intimately linked, with aggressive males dispersing further than less-aggressive males. Aggressive males harass females which results in reduced female fecundity and increased female mortality. When male mating aggression increases in local frequency,

mating activity and female fecundity decline (Sih & Watters, 2005; Eldakar et al., 2009b). As such, in isolated pools, where aggressive males cannot escape the consequences of local exploitation, aggression should decrease over time. Eldakar et al. (2010) found that populations inhabiting the limited dispersal regimes of free-flowing ephemeral streams were significantly less aggressive than those of the free-flowing perennial streams, which allow aggressive males to move more freely and to escape the group-level costs of their aggression. These findings support the relevance of relating the behavioural differences of natural populations to corresponding differences in their population structures.

### **Conclusions and future directions**

We hope that this issue will spark interest in the importance of considering the individual's immediate social environment — i.e., the impact of competition through population-density effects and resource availability — on the amount of interactions with other individuals to understand the plasticity and adaptability of an individual's behaviour in natural systems. Understanding how individuals respond to changes within their own specific environment is, therefore, crucial to our gaining insight into how individuals, populations and species respond to environmental change. In this issue we present studies that demonstrate how the social environment affects individual dispersal and settlement and mate-choice decisions, and with that the consequences for individual fitness. However, it should also be clear from these studies that it is difficult to completely investigate the effect of an individual's social environment and the adaptiveness of an individual's behaviour in a single species. A common difficulty is moving beyond the observation that (local) environmental conditions influence individual behaviours to investigating causal and functional significance. First, there are many other potential causes of changes in individual behaviours rather than the social environment, such as maternal, genetic and ontogenetic influences on behaviour (e.g., the early social environment). Some studies in this issue have shown that the expression of social behaviour is not always plastic (van Dijk et al., 2010; Richardson et al., 2010). There is good evidence that in some species the “switch” mechanism between different types of social behaviour is genetically or maternally regulated. The challenge lies in separating out the different components of the environments and specifically, the combined roles that social

environment and densities play in determining the selection pressures faced by individuals and, therefore, their evolution. Second, studies are often observational, rather than experimental, and this presents the usual problems with respect to assuming causality. These sorts of experiments are challenging to carry out as they require large-scale manipulations of population density and/or local sex ratios. Third, many studies of environmental related changes in social behaviour draw strong inferences about the adaptive value of behavioural strategies, without sufficient information to precisely quantifying fitness pay-offs. Most studies only investigate the short-term fitness consequences (e.g., yearly survival, number of fledglings produced, or young recruited into the population) and do not account for extra-pair paternity. Because social interactions underlie almost all of the processes that result in fitness variation, it is important to monitor the long-term inclusive fitness effects induced by changes in social environments. For this one needs long-term pedigree studies to quantify lifetime reproductive success. This requires the ability to monitor dispersal and settlement decisions and the reproductive output of individuals from birth to death. This is extremely difficult, because for the vast majority of populations these data are not available. Future work should include experimental manipulation of breeding densities and local environmental factors, and monitor the long-term fitness consequences of these environmental changes. This will be very timely and difficult to carry out in the field. There are few if any studies that have experimentally manipulated the social environment, either in the lab (Heg et al., 2010) or in the wild (Nicolaus et al., 2009; Alonzo & Sheldon, 2010). One study that employed large-scale field manipulations of demographic parameters (density and sex ratio) and monitored individual behaviour and long-term fitness is that on great tits (*Parus major*; Nicolaus et al., 2009). However, despite a large scale experimentation it is extremely difficult to precisely quantify an individual's inclusive lifetime fitness as a consequence of specific aspects of the social environment. Measuring fitness consequences is challenging, because their effects might only be apparent after long-term monitoring of interrelated aspects of the social environment. Here, recent developments of accurate short-term measures of fitness may help (for more details, see Coulsen et al., 2006; Brommer et al., 2007).

We hope that this issue will promote the development in our understanding of the role of the social environment on the expression of individual behaviour, which is necessary to understand adaptation. It should also be clear

that individual variation in behaviour could be genetically or maternally influenced, and therefore it is important to integrate studies of environmentally mediated behaviour with research on genetics, maternal and ontogenetic influences on behaviour (e.g., the early social environment).

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