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 Kluyver & 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