

REVIEW

Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations

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Abstract

Over the past 40 years, the study of animal populations has shifted from a relatively simple science that assumed the most crucial regulating mechanisms were the intrinsic properties of breeders, to a more complex and refined discipline that reflects a greater understanding of populations and their dynamics. Part of this shift has been the explicit recognition of the importance of a previously overlooked nonbreeding component of animal populations, the so-called *floaters*. Here we review and discuss the various effects that pools of floaters can have on the structure, dynamics and persistence of bird populations. Under some circumstances floaters can be both active intruders that can alter the breeding performance and behavioural traits of territory owners, as well as secretive presences reducing the extinction risk of populations. Floaters are crucial elements in conservation biology, and knowledge of their behaviour and dynamics in avian communities can be a key factor in the success of conservation strategies. Firstly, larger pools of floaters are associated with more stable breeding populations, even in cases where breeding output could be impacted through interference by floaters. Secondly, the effects of habitat loss and mortality rates are frequently ignored in areas where floaters settle, and consequently conservation measures tend to overlook these sites, potentially leading to increased risks of mortality among floaters. Thirdly, because an increase in the proportion of juveniles in the breeding component of a population may be because of increased pre-adult and/or adult mortality rates, a change in the age of breeders has the potential to function as a warning of an imminent decline in breeding populations. Most population studies have only considered the breeding components of animal populations, so it is time now to focus attention on the floater component, wherein the solution to many conservation issues may be found.

Floating birds in days long past

Darwin (1871) was the first to describe the occurrence of wandering male birds, but the idea that nonbreeding individuals are a consequence of the territorial spacing of breeding pairs was initially expressed by Moffat (1903), who was the first to understand the important role of floaters in buffering breeder numbers. These initial ideas were later synthesized by Brown (1969). Probably because the first indirect evidence for the existence of floaters was the rapid replacement of territorial owners following their experimental removal (reviewed in Newton, 1992), floaters were initially consid-

ered to be subordinate individuals who passively wait for opportunities. In the 1970s, when specific research on floaters first began, they were still perceived to be 'renegade' individuals: nonbreeders were essentially considered unsuccessful competitors who had been excluded from breeding territories by higher ranked individuals, and/or individuals leading a wandering existence with no fixed areas of residence or social organization (e.g. Krebs, 1971; Stutchbury & Robertson, 1985; Eckert & Weatherhead, 1987). However, this idea was challenged at the end of the 1970s by Smith (1978), who introduced the concept that floaters are individuals (1) living in a different social system; (2) able to

compete, fight for territory and mate when necessary. By showing the peculiarity of floater life, Smith (1978, 1984) introduced new perspectives in investigations of floaters.

The origin of floaters: territoriality and habitat saturation?

Floaters were initially defined as birds prevented from breeding by territoriality or other spacing behaviours (Brown, 1969; Smith, 1978; Newton, 1992; see also the conceptual review of Winker, 1998); that is, resource availability limits the number of breeders, and territory competition makes some individuals become floaters when all suitable breeding habitats are occupied. Whereas the 'individual-saturation scenario' is central to the theory of floaters, the reality is often more complex (Smith & Arcese, 1989; Blas & Hiraldo, 2010). Evolutionary aspects of the floater strategy are reflected, for example, in delayed maturation, leading to greater fitness than that occurring with early breeding. Floaters may also be individuals who reject all vacant breeding locations, preferentially waiting for access to a higher quality site that may increase their fitness (e.g. floaters queuing for a focal territory; Kokko & Sutherland, 1998; Pen & Weissing, 2000; Kokko, Harris & Wanless, 2004; Bruinzeel, van de Pol & Trierweiler, 2006; van de Pol *et al.*, 2007).

Under some circumstances a floater may shift from being a secretive presence within an occupied territory (Rohner, 1997; Delgado *et al.*, 2009; Campioni, Delgado & Penteriani, 2010) to become an active intruder that seriously threatens the position of the 'owner' of the territory (Arcese, 1987). In such cases floaters can become a drain on breeders, mainly because: (1) owners may spend a great deal of time and energy chasing floaters from their territories (Sunde & Bølstad, 2004; Carrete, Donazar & Margalida, 2006a), with floater intrusions representing an additional cost during reproduction (Birkhead, 1982; Sandell & Diemer, 1999; Pilz & Smith, 2004; Bretagnolle, Mougeot & Thibault, 2008); (2) high levels of floater pressure may oblige owners to reduce the sizes of their territories (Norton, Arcese & Ewald, 1982); (3) floaters may compete for food with territory owners; (4) in some species (notably raptors) the intruders can kill owners in territorial fights (Newton, 1979).

The link between floaters and breeders is not purely that of immigration and emigration rates (Hogstad, 1990), as floaters are cagey individuals who use sophisticated strategies to augment their future breeding opportunities (e.g. Matthysen, 1989; Brotons, 2000; Piper *et al.*, 2006). Each breeder was previously a floater, and its experiences during the wandering period have the potential to influence the characteristics of the breeding population. All factors (individual, biotic and abiotic, habitat related, random events) affecting floaters before they become an active part of the reproductive population will shape the features of the population they enter (e.g. health, age structure, breeding performance, habitat selection, dispersal directions; see also Penteriani & Delgado in press). Ens, Weissing & Drent (1995, 646–647) noted that '... the observed distribution of

territorial birds cannot be understood from measurements on the territorial owners only but must include their years of battle as nonbreeders'. With such a variety of scenarios and behavioural strategies the question arises: what exactly are floaters?

What exactly are floaters?

Floaters are multifaceted population members that are better understood when considered in three nonexclusive (and frequently interacting) contexts: (1) the ecological scenarios underlying breeding population dynamics; (2) the process of natal dispersal; (3) the age cohorts contributing to floater pools. Because of the diverse contexts of studies on floaters, the definition of this term varies and shifts over time. The differences do not represent dissimilar or contradictory perceptions of the floater status, but rather reflect the fact that it can differ depending upon the situation and other constraints.

Floaters are individuals able to enter the reproductive population as breeders when a breeding site or potential mate becomes available (Penteriani, Otalora & Ferrer, 2005a, 2006b, 2008). A potential mate can be both (1) the owner of a suitable breeding territory; (2) in nonterritorial species, a lone mate available for reproduction. This definition highlights that floaters are sexually mature individuals. As potential breeders contributing to population fecundity and dynamics, the role of floaters commences when they are ready to reproduce. Floating individuals moving close to or within breeding areas may also (but not necessarily) be considered to be dispersers, although the definitions of floaters are not commonly based on their dispersal status. However, if we accept the most general definition of natal dispersal (i.e. the movement of an individual from the natal area to the area where breeding first takes place; Clobert *et al.*, 2009), then floaters may also be considered dispersing individuals until they first reproduce. Therefore, individuals floating around breeders conserve their disperser status because dispersal movements are not restricted to a specific distance range (e.g. Delgado & Penteriani, 2008). Resident floaters around the breeding sites of the reproductive fraction of the population can be considered highly philopatric dispersers.

From a demographic point of view, more restrictive ranges or limits should be fixed when considering the age of floaters and their stage of sexual maturity. Firstly, because survival rates of adults and juveniles tend to differ (i.e. we expect survival rates of juveniles to be lower than that of breeders), the floater-to-breeder ratio would become dependent on time-of-year if juveniles are included in the floater definition (e.g. a sudden change in floater-to-breeder ratio would follow new births). Finally, the floater-to-breeder ratio would vary with annual cohort size, which may fluctuate widely and with no relationship to the specific floater ecology. As an end result, and under the perspective of population demography, there are good reasons to define floaters as adults without breeding territories, and to regard the aggregate of floaters and juveniles as 'nonbreeders'.

Moreover, whereas nonbreeding juveniles may only compete with breeders for food, when juveniles reach sexual maturity they may represent an additional pressure on breeders if they compete with owners for territory or mate (López-Sepulcre & Kokko, 2005).

In addition, sexually mature individuals that are owners of a breeding territory can also shift from breeder status to floater status if evicted from their territory by an intruder. In this case a former floater that had acquired (and then lost) the status of a territory owner may return to floater status as it searches for new breeding opportunities (Kokko *et al.*, 2004).

In conclusion, depending on the ecological and behavioural context in which animal populations are considered, the term floater can have different and nonexclusive meanings and implications (see also Hogstad, 1990).

How the fate of floaters can affect the stability of breeding populations

More than 50 years ago, Brown (1969) first recognized the value and contribution of floaters to bird populations, and highlighted the importance of considering floaters as a well-defined component of animal populations, with specific sizes, distributions and dynamics from year-to-year. More than a decade later, floaters had come to be recognized as an essential element in the regulation of population structures, trajectories, spatial–temporal distributions and stability and important to the extinction risk of populations; studying floaters was accepted as central to gaining a complete understanding of population dynamics (Jamieson & Zwickel, 1983).

From the perspective of conservation biology the absence of information on floaters may lead to misleading conclusions about population health and persistence. Franklin (1992) was one of the first to show that a decrease in the number of floaters in a declining population may take several years to be detected in the breeding population. Moreover, a decrease in the floater populations may not be detected by traditional monitoring programmes, which are typically based on breeding territory censuses (Wilcove & Terborgh, 1984; Rohner, 1996).

An important concept first introduced by Newton (1988) and later discussed by Hunt (1998) is the floater-to-breeder ratio. This is a key parameter that allows researchers to assess the health of an animal population and the potential for the population to act as a source of recruits to other populations. Newton (1988) observed that for peregrine falcons *Falco peregrinus* a ratio of one or more floaters to one breeder could be expected for healthy populations, and that larger pools of floaters were associated with more stable breeding populations, even when breeding output was potentially impacted by floater interference (Hunt, 1998).

Kokko & Sutherland (1998) were among the first to show that floaters act as an important buffering pool of individuals, but that this is very difficult to quantify. This impacts not only our understanding of how and why animal populations fluctuate, decrease and disappear, but also our knowl-

edge of where extinction factors act on a population. Most research to date on population dynamics has focused on mortality among breeders and the impact of persecution and habitat loss on the dynamics of breeding communities. The effects of habitat loss, mortality rates, extinction probability and environmental stochasticity are typically ignored or considered to be less important in relation to settlement areas (i.e. stable zones, occupied by floaters for the longest time period across the whole dispersal process or until they become owners of a breeding territory). As a consequence, conservation measures tend to overlook such sites, potentially leading to increased mortality risks for dispersing individuals. Moreover, because dispersal displaces individuals across unfamiliar terrain, losses during dispersal are likely to be considerable. As a result, habitat destruction and decreased survival rates in settlement areas could be critical factors affecting the persistence of the entire population, potentially making the species more vulnerable to extinction as a consequence of demographic and environmental stochasticity.

Penteriani *et al.* (2005b) drew attention to a ‘perverse butterfly effect’ resulting from the impact of increased floater mortality on the breeding population. Because productivity in the breeding population is generally a density-dependent property of the breeder pool, this parameter tends to be less sensitive to an initial increase in floater mortality. When mortality is high in floater settlement areas, pair formation becomes increasingly difficult because of the lack of new individuals available to replace lost mates. The worst consequence of this scenario is that at the beginning of a population decline resulting from a major loss of floaters, relatively stable breeding performance could generate the false impression that the population is healthy, even if some breeding territories are lost. Moreover, because the less frequently occupied and most easily deserted territories are generally of the lowest quality, such an early warning signal could easily go unnoticed. Finally, increased floater mortality could appreciably impact the breeding part of the population after some years, when the decline accelerates (Penteriani *et al.*, 2005b). This implies that it may be unwise to monitor only the breeding part of a population because of the potential delay in detecting a decline, underestimating the extent of a decline and overestimating recovery levels (Kokko & Sutherland, 1998; Kenward *et al.*, 2000). More generally, Penteriani *et al.* (2005b, 2006a) found that: (1) the survival of dispersing individuals (the numbers of which depend on the productivity in breeding areas) is highly dependent on the number of available settlement areas and their resources; (2) environmental stochasticity has a greater influence on the entire population (breeders + floaters) when variations in environmental conditions occur in a synchronous way (i.e. simultaneously in both the settlement and breeding areas).

Many factors that influence population dynamics have their origins in local processes acting on subunits of the entire population; some are linked to the way dispersal affects demography in breeding territories and can have a profound impact on the persistence of the entire population.

Therefore, conservation strategies should view populations as stratified systems comprising a network of smaller sub-units, for example dispersers and breeders, or settlement and breeding areas, the persistence of which is not only dependent on the local dynamics within each breeding unit, but also on the probability that floaters survive dispersal each year and are integrated into the reproductive portion of the population, relative to the number of individuals that die in both settlement and breeding areas (Rutz & Bijlsma, 2006).

Human-induced mortality may also represent a locally significant constraint on avian populations. When direct persecution or less obvious, destabilization of a population (e.g. mortality caused by power lines or the illegal use of poison; Sergio *et al.*, 2004; Oro *et al.*, 2008) acts on the breeding population, the availability of a healthy floater pool is critical to persistence of the entire population. In fact, the availability of floaters may make the difference between a stable population and a declining population approaching the extinction threshold (Penteriani *et al.*, 2005b; Oro *et al.*, 2008).

As most bird species exhibit age-specific patterns of breeding performance, with fecundity generally increasing with age (Proaktor, Milner-Gulland & Coulson, 2007), the sudden addition of numerous juveniles to a breeding population experiencing high anthropogenic mortality may also decrease its breeding performance (Balbontín, Penteriani & Ferrer, 2005). If human-induced mortality in a breeding population is very high, the addition of many young, inexperienced and formerly nonbreeding individuals into such a population could lower the reproductive output of the population as a whole (Carrete *et al.*, 2006b).

Density-dependent regulation of bird populations and the Allee effect

Density dependence is one of the key processes regulating bird population dynamics and stability (Turchin, 1995; Newton, 1998; Sibly, Hone & Clutton-Brock, 2003). The strong relationship between floaters and breeders of the same population suggests that floater dynamics in settlement areas may affect breeding population mechanisms, including density dependence. However, most studies on density dependence in animals have focused primarily on the breeding populations, and have generally ignored the possibility that nonbreeder mortality has the potential to affect demographic rates (Penteriani *et al.*, 2009).

High floater mortality may decrease the number of breeders, leading to a positive density–fecundity relationship in the breeding portion of a population (i.e. the Allee effect; see the review in Penteriani, Otalora & Ferrer, 2008). Under this scenario a floater perspective may be a novel way to approach such a mechanism of declining populations (Penteriani *et al.*, 2008). Although the Allee effect relates to the breeding portion of a population, the extinction process starts because of the scarcity of available mates (the most common cause of the Allee effect), and this can have its origin in high floater mortalities in settlement areas. Thus, simply knowing that the Allee effect is threatening a popula-

tion may not be informative of a solution: the source of the problem must also be understood (e.g. floater settlement areas) and conservation efforts directed there.

Increasing rates of floater acquisition of breeding territories as a warning signal of population declines

Some species have been able to recover from human-induced mortality through high levels of recruitment of juveniles floating around the breeding populations (e.g. Wyllie & Newton, 1991). Little information is available on the age composition of floaters (but see Sergio, Blas & Hiraldo, 2009), although it is generally accepted that nonbreeding components of populations are mainly composed of juveniles (Newton, 1991, 1992; Rohner, 1996). Consequently, pools of juvenile floaters are especially important in species for which the age at first breeding is early or can decrease when the availability of breeding territories increases (Ferrer, Otalora & García-Ruiz, 2004).

Franklin (1992) provided what appears to be the first evidence that a reduction in the average age of breeders, in particular due to an increase in the proportion of juveniles in the breeding population (which may arise from increases in the pre-adult and/or adult mortality rates), can function as a warning signal of an imminent decline in stable breeding populations. This underscores the importance of monitoring not just the numbers and locations of breeders, but also their ages. This is an essential concept in conservation biology: monitoring the composition of recruits from the floating population may allow early prediction of a future population decline at a time when it might still be possible to prevent the decline (Kenward *et al.*, 2000; Ferrer *et al.*, 2003). Although regular monitoring of the age structure of territorial pairs may not be feasible in species for which age cannot easily be established, this is a potentially reliable method for forecasting changes in population viability in many other species, and provides a useful tool for improved conservation biology. Such monitoring may well have better predictive power than the simpler and more common annual surveys involving counting of the number of breeding pairs.

An interesting conclusion can be drawn from data on floater recruitment in populations undergoing breeding population decline. Franklin (1992) proposed that if breeder numbers decrease significantly, the floating population could become exhausted through increased recruitment to the breeding population. More than 15 years later, Ferrer & Penteriani (2008) provided empirical evidence showing how a population that initially increased and then stabilized could later approach extinction because of the dual effects of increased breeder mortality and consequent low availability of floaters to replace all the lost breeders. A high rate of recruitment of floaters because of high mortality among breeders would have the same effect on a population as an increase in floater mortality, because of the increasing difficulty of replacing a lost mate. In fact, while floaters can enter the reproductive population as new breeders when

breeder mortality increases, this recruitment may not be sufficient to enable the population to increase to a stable or saturated level because of extremely high adult mortality (i.e. the floater pool is not sufficient to replace all of the lost breeders).

Breeding areas versus temporary settlement areas: a lesson for conservation biology

In view of the key role of floaters in avian populations, it is important that conservation plans be directed at settlement areas. As disperser settlement areas are generally unknown or difficult to detect, less effort is typically devoted to the conservation of these sites. Population studies, analyses of population viability and extinction risk assessments that ignore the dynamics of dispersers in settlement areas may fail to establish how and why animal populations decrease, and may consequently lead to inappropriate or ineffective conservation actions (Penteriani *et al.*, 2005b; Oro *et al.*, 2008).

Breeders and floaters may occur in different habitats. Breeders locate in places that offer food and nest sites, whereas nonbreeders are frequently found in places that offer food but not necessarily nest sites. Recent evidence (e.g. Delgado *et al.*, 2010; see also Fig. 1) indicates that: (1) dispersers may use areas in which high levels of anthropogenic disturbance result in high mortality rates; (2) settlement areas can look very different from breeding areas (Fig. 1). Thus, although apparently low value areas are not typically considered in conservation plans, they may be inhabited by the majority of floaters waiting for opportunities in breeder habitat. Therefore, because conservation efforts targeting endangered species and/or populations focus on breeding areas or nesting sites, they may be ineffective if the real problem is in the settlement areas. As a result, human and financial efforts may be wasted in locations other than those in which the conservation measures are really necessary. In fact, declines in breeding

population size could divert attention from critical problems in the floater pool. Conservation biology in the future should consider nonbreeding habitats that play a critical role in the larger-scale persistence of the species, as well as winter floaters and wintering areas (Brown & Long, 2007). In the absence of this focus there is a risk of underestimating threats to a species/population where the main problem is not in the breeding territory, but where the effects of floater mortality are sooner or later likely to impact on breeder numbers. Therefore, for the majority of species the absence of information on the location of settlement areas and the dynamics of individuals in them may leave conservation efforts ill-equipped to halt population declines.

Because the presence of floaters is not generally evident, they may also act as 'invisible' intraguild predators on endangered species in settlement areas: intraguild predation has generally been studied only within breeding populations (Lourenço *et al.*, 2011). Thus, estimates of the effects of intraguild predation that do not account for the impact of floaters on their intraguild prey may greatly underestimate floater predation impacts within animal populations.

Conclusions: floaters, necessary but sometimes hostile

Over recent decades researchers have increasingly focused on understanding the behavioural mechanisms underlying floater survival, and the relationships between floaters and territory owners. The earliest studies focused largely on the floater population in terms of age classes, individual quality, and the hierarchical position of floater individuals. Researchers subsequently began to investigate the characteristics of floater home ranges, their strategies for becoming breeders and the nature of the contests that can arise when an owner detects an intruder or a floater actively tries to force an owner to leave its territory. Over time it became evident that floaters can buffer, regulate and stabilize breeding populations, not just interfere with the reproductive activities of owners. In fact, the presence of a reservoir of



Figure 1 Breeding versus settlement areas. The areas occupied by breeders and floaters can be extremely dissimilar. This is exemplified by differences in the landscape between a breeding site (a) and a floater settlement area (b) of the eagle owl *Bubo bubo*. The differences may cause serious mistakes in species conservation: breeding areas, both for major wilderness and because breeders are generally easier to detect than floaters, are easier to protect than the human-altered habitats commonly associated with settlement areas. In the latter, the risk of mortality may be extremely high because of a variety of impacts including electrocution, car collisions and shooting.

individuals that can quickly replace breeders allows breeding numbers to remain stable (Walters, Crowder & Priddy, 2002; Grimm *et al.*, 2005). As also stressed by Pontier *et al.* (2008), floaters may have very important consequences for the stochastic extinction of bird populations, through a mechanism known as the buffer effect (Grimm *et al.*, 2003, 2005). Because bird numbers may exhibit important inter-annual variations (due to both environmental and demographic stochasticity), the presence of a pool of sexually mature individuals that do not breed acts like a buffer, allowing to compensate for losses in the subpopulation of breeders and, consequently, to improve their persistence probability.

The words of one of the first researchers fascinated by floaters (Brown, 1969, 313–314) highlights their complex world and role within animal populations: ‘... the surplus becomes a predictable feature of the environment of the population and the possibility of evolutionary adaptation to it emerges’. That is, the (breeding) population may show specific adaptations to the presence of a persistent floater pool close to or within breeding areas, and consequently floaters can be a fundamental evolutionary force shaping the attributes of the entire population.

Some of the characteristics of bird populations that, in addition to other evolutionary pressures, may reflect adaptations/strategies to the largely ‘invisible’ but significant floater component of populations include delayed maturation and changes in plumage from juvenile to sexually mature individuals, migration habits and rates of philopatry, clutch sizes and sex ratios, year-round territoriality, territory sizes and home-range overlaps (as a trade-off between the ability to defend a territory from intruders and having a territory with sufficient resources), group territoriality (where additional members of family groups aid in the detection and chasing of intruders), and degrees of mate fidelity and polygyny (as an evolutionary adaptation to the contemporaneous availability of surplus potential mates).

The study of floaters and its implications for species and population conservation is just beginning. By exploring the ‘tip of the iceberg’ of the importance of floaters, researchers have highlighted several unexpected but crucial elements which, if integrated into conservation strategies, may affect the survival of avian populations. There are three main areas of research with the potential to lead to major new discoveries and insights, and to substantially improve conservation outcomes. (1) More information is needed on the interactions between floaters and breeders (e.g. the role of interference behaviour in population regulation). This has the potential to provide new and practical tools for population management and conservation (Bretagnolle *et al.*, 2008); (2) we lack information on how differing social systems may influence the relationships between floater individuals and territory owners. For example, we can hypothesize that floaters of colonial or semicolonial bird species or populations will have different strategies (e.g. when prospecting available breeding territories and mates) to solitary birds (e.g. Anderson *et al.*, 2002, 2003; Imber *et al.*, 2005; Dittmann, Ezard & Becker, 2007; Jenouvrier

et al., 2008), which will determine the application of various conservation measures; (3) we need better empirical data (including biological models involving more diversified life histories) to improve our knowledge of and ability to predict population stability, persistence and extinction risks.

Finally, we note that research is changing the negative perception of floaters as inconvenient competitors of breeders to one of an important population component that, depending on circumstances and scenarios, represents a pool of individuals about which an understanding is crucial if the future persistence of avian populations is to be assured.

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