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THE UNKNOWN LIFE OF FLOATERS: THE HIDDEN FACE OF SEXUAL SELECTION

LA DESCONOCIDA VIDA DE LOS FLOTANTES: LA CARA OCULTA DE LA SELECCIÓN SEXUAL

Juan MORENO¹ *

SUMMARY.—Sexual selection, as a form of social selection based on reproductive resources, is a crucial driver of evolutionary change. Many studies on sexual selection identify potential targets only within the reproductive fraction of populations. Floaters constitute the non-territorial fraction of the population, according to the usual definitions. Floaters have been identified through exhaustive capture and marking programmes, removal and nest-box addition experiments, extra-pair paternity studies, acoustic marking and genetic studies. The literature shows that floaters may represent a considerable fraction of populations, especially among males. There is no clear evidence that size, condition or testosterone level is necessary for explaining floater status generally. However, the literature suggests that ornament size and expression are involved in territorial exclusion and may be either its cause or one of its consequences. There is some evidence that floaters survive and reproduce less well than territorials, and that changes from floater to territorial status are accompanied by changes in survival and reproductive rates. However, certain male floaters may obtain some reproductive success through extra-pair copulations. The possibility that floating constitutes a successful alternative strategy in some species cannot be excluded, although the current preliminary consensus is that floaters are ‘making the best of a bad job’. Floater status may be imposed by limitations in the availability of mates or breeding space resulting in skewed population sex ratios, polygamous mating systems, high population densities and increased demand for specific breeding requirements such as space in colonies or adequate nesting cavities. Predictions concerning the effects of these factors have not been conducted to date. Few studies have been able to clarify the duration of floater status in any population. For short-lived species, floater status in a single breeding season may in fact imply zero lifetime reproductive success. In males, the existence of a considerable fraction of floaters attempting to breed may select for intense territorial behaviour and competitive mate guarding tactics in territory holders and in aggressive extra-pair copulation and territory acquisition tactics in floaters. Interference competition from floaters may lead to density-dependent declines in reproductive success. In females, the attempts by floaters to attain breeding opportunities may have contributed to the observed propensities for female prospecting and for female-female aggression and the signalling of female dominance towards other females. Moreover, there may exist selection in females for signalling quality to mates in order to avoid being evicted by

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rivals. Excluding floaters from the analysis of sexually selected traits may severely affect sexual selection estimates because of biased sampling for large or more intensely expressed ornamentation. The importance of sexual selection may be negated or underestimated when in fact its action on floaters could be maintaining current levels of expression in the territorial fraction. Existing phenotypes should express, in their morphology, physiology and behaviour, the relentless drive through evolutionary time to avoid becoming a floater.

Key words: extra-pair paternity, ornaments, population density, reproductive resources, territoriality.

RESUMEN.—La selección sexual como forma de selección social basada en recursos reproductivos es un importante motor del cambio evolutivo. Muchos estudios de selección sexual identifican objetivos potenciales solo en base a la fracción reproductiva de las poblaciones. Los flotantes constituyen la fracción no territorial de la población según las definiciones al uso. Los flotantes han sido identificados por medio de programas exhaustivos de captura y marcaje, experimentos de retirada de individuos o de nidales, estudios de extrapaternidad, marcaje acústico y estudios genéticos. La bibliografía muestra que los flotantes pueden representar una fracción considerable de las poblaciones estudiadas, especialmente en los machos. En general, no hay evidencia clara de que el tamaño, la condición o el nivel de testosterona sea crucial para determinar el estatus de flotante. Sin embargo, los datos existentes apuntan a que el tamaño y la expresión de los ornamentos están implicados en la exclusión de los territorios y pueden ser su causa o una de sus consecuencias. Existe alguna evidencia de que los flotantes sobreviven y se reproducen peor que los territoriales, y que cambios de flotante a territorial se acompañan de cambios en las tasas de supervivencia y reproducción. Sin embargo, algunos machos flotantes pueden obtener cierto rédito reproductivo por medio de cópulas extrapareja. La posibilidad de que los flotantes representen una estrategia alternativa exitosa en algunos casos no se puede descartar, aunque el consenso preliminar actual es que los flotantes ‘hacen de la necesidad virtud’. El estatus de flotante puede ser impuesto por limitación de parejas potenciales o recursos para reproducirse en relación con razones de sexo sesgadas en la población, sistemas de apareamiento poligámico, elevadas densidades poblacionales o requerimientos específicos para criar como espacio en colonias o cavidades de nidificación adecuadas. No se han comprobado hasta la fecha predicciones basadas en los efectos de estos diferentes factores. Pocos estudios han sido capaces de esclarecer la duración del estatus de flotante en cualquier población. Para especies de vida corta, el estatus de flotante en una sola temporada reproductiva puede de hecho representar un éxito reproductor vital nulo. En machos, la existencia de una considerable fracción de flotantes intentando reproducirse puede seleccionar a favor de conductas territoriales extremas y tácticas competitivas de protección de la pareja en individuos territoriales y a favor de tácticas agresivas de obtención de cópulas extrapareja y de adquisición de territorios en flotantes. La competencia de interferencia por parte de flotantes puede conllevar reducciones en éxito reproductor dependientes de la densidad. En hembras, los intentos por parte de flotantes de obtener oportunidades reproductivas pueden haber contribuido a las conductas observadas de prospección y agresión entre hembras y la señalización de dominancia sobre otras hembras. Además puede existir selección en las hembras a favor de señalar calidad a sus parejas para evitar ser expulsadas por hembras rivales. La exclusión de los flotantes del estudio de rasgos sexualmente seleccionados puede afectar seriamente las distribuciones a explicar al sesgarlas hacia mayores tamaños de ornamentos o expresiones más intensas de los mismos. La importancia de la selección sexual puede ser negada o subestimada cuando de hecho su acción sobre los flotantes podría estar manteniendo los niveles presentes de expresión en la fracción territorial. Los fenotipos existentes deben expresar en su morfología, fisiología y conducta la presión constante a lo largo del tiempo evolutivo para evitar convertirse en flotantes.

Palabras clave: densidad de población, ornamentos, paternidad extrapareja, recursos reproductivos, territorialidad.

INTRODUCTION

Sexual selection as a form of social selection based on reproductive resources is a crucial driver of evolutionary change (Darwin, 1871; West-Eberhard, 1983). There is some current debate concerning the fitness components linked to sexual selection (Cain and Rosvall, 2014). Some authors define sexual selection as only related to pure mating advantages (Lyon and Montgomerie, 2012), regarding other forces linked to intraspecific competitive processes as social selection (following West-Eberhard, 1983). However, for simplicity we here define sexual selection as based also on advantages related to fecundity. Given the overlap between traits involved in acquiring and defending mates and other resources necessary for reproduction, the difference between the two forms of selection may be rather semantic (Lyon and Montgomerie, 2012). Although the origin of sexual selection in its widest meaning lies in competition for access to gametes in anisogamous organisms, it has been transformed during evolution into a complex force scrutinising each and every organismic trait for its potential effect on mating and breeding success (Andersson, 1994). Many studies have been devoted to identifying the traits that are being sexually selected and to clarifying the strength of selection based on acquisition of reproductive resources. These resources include not only gametes and adequate pair mates but also the territories or nesting sites that are essential for reproduction. Traits that promote success in the acquisition of reproductive resources can be morphological, physiological or behavioural, or express a combination of aspects of phenotypes. They can serve to exclude competitors from available resources through aggression or signals of social dominance, but also to attract potential mates in a social or purely sexual context. They can be expressed in both sexes, depending on the

relative strength of competition for reproductive resources operating in males and females (Tobias *et al.*, 2012). Although males have traditionally been considered as the sex that experiences the strongest sexual selection, due to the intrinsic constraint arising from different rates of gamete production, females may also have to compete for resources other than the gametes necessary for successful reproduction, such as mates, territories or nesting sites. Thus, it is not obvious that the traits expressed by females in contests for reproductive resources are merely carry-over effects from selection on males (Tobias *et al.*, 2012).

Many studies on sexual selection identify potential targets in the reproductive fraction of populations. Typically, they compare the success obtained in mating or offspring production by adult phenotypes in a breeding population and estimate selection differentials (e.g., Garant *et al.*, 2004; Møller and Szep, 2005; Hegyi *et al.*, 2006). This is the correlative or descriptive approach that has supported the importance of sexual selection for the evolution of morphological, physiological and behavioural phenotypes in many populations. Alternatively, other workers have conducted experiments in which they have manipulated the expression of morphological or behavioural attributes to try to register their importance for mating and reproductive success (Andersson, 1982; Møller, 1988). Usually, individuals have been caught in their breeding territories or at their active nest sites in order to manipulate their phenotypes. In both the descriptive and experimental studies, research has dwelt on the phenotypes of breeders or at least of territorial individuals. However, there is a fraction of adult individuals in most populations that do not reproduce during a proportion of their lifetimes (Newton, 1998). In birds such as crows, swans and waders, non-breeders occur separately in flocks and can be readily observed and counted (Carrick,

1963; Harris, 1970; Holmes, 1970; Patterson, 1980). In others, such as many songbirds and raptors, some individuals live secretive lives in and around the territories of breeders or move continuously from one place to another (Kendeigh, 1941; Delius, 1965; Smith, 1978; Newton, 1979; Rohner, 1997; McNabb *et al.*, 2007; Tanferna *et al.*, 2013). This fraction of unmated, non-territorial individuals that are difficult to observe and count is defined by the term ‘floaters’ in the literature (Winker, 1998). The importance of floaters for population processes and conservation biology has been recently reviewed in the literature (Lenda *et al.*, 2012; Penteriani *et al.*, 2011). There is agreement that the usual neglect of this population fraction in the ecological literature may seriously undermine our understanding of many aspects of natural populations. Sexual selection is no exception in this context, as floaters may constitute the strongest expression of its strength in not merely reducing but annulling the reproductive success of certain individuals. Just comparing the phenotype-dependent success of the breeding or territorial fraction of populations in comparative or experimental studies is insufficient for understanding the force of a process in promoting competitiveness in reproductive contexts. This systematic undervaluation of sexual selection has been covered by recent reviews (e.g. Lenda *et al.*, 2012) but has not yet received full attention from researchers. Here we concentrate on avian populations, for which knowledge on floaters remains scant. We only analyse breeding season floating, excluding all studies on winter floating (reviewed by Brown and Long, 2007). Given the existence of recent reviews on the importance of floaters for population dynamics (Newton, 1998) and conservation biology (Penteriani *et al.*, 2011), this review only examines the implications for studies of sexual selection. No phylogenetically controlled comparative analyses have been

conducted due to the paucity of information available and the strong taxonomic bias in the literature towards certain taxonomic groups, such as passerines.

FLOATERS AND NON-BREEDERS

Floaters constitute the non-territorial fraction of the population, according to the usual definitions. Territorial status is used here in its widest meaning, including ownership of any resource necessary for breeding such as adequate space in a breeding colony, display space in a lek or an adequate nesting cavity. However, this fraction is composed partly by juveniles who have not attained the condition or experience necessary for initiating breeding activities (Cooper *et al.*, 2009; Bayne and Hobson, 2001; Rivera *et al.*, 2011; Mumme, 2015). These juveniles may routinely end up breeding as they mature (Newton and Rothery, 2001; Sergio *et al.*, 2011; Rivera *et al.*, 2011; Loewenthal *et al.*, 2015) and hence are only temporarily excluded from the breeding fraction of the population. Moreover, being juvenile floaters may be the general pattern for most individuals and not a characteristic of a particular fraction (Delgado *et al.*, 2009; Ryder *et al.*, 2011). Thus, excluding such floaters from analyses may not seriously affect an evaluation of the strength of sexual selection. However, floaters also include adult individuals that do not breed for part or all of their lifetimes (Shutler and Weatherhead, 1991; Reitsma *et al.*, 2008; Villavicencio *et al.*, 2013). This fraction is defined by the non-acquisition of territories, which leads to their floating behaviour. For logistic reasons most studies deal with territorial birds that may be located and captured for phenotypic measurements. It is thus obvious that they are missing part of the picture by excluding floaters. The question is whether all floaters are non-reproductive, as emphasised by cer-

tain definitions. Assigning uncategorised birds to the resident territorial fraction on the basis of adult plumage (e.g., Morton *et al.*, 2000) is questionable as it assumes that all floaters must be juveniles. We hereafter refer only to non-juvenile floaters. Future studies should attempt to identify the fraction of adult floaters as others (e.g., Butchart, 2000) have done.

To exclude cases in which floaters obtain reproductive success by means other than territory acquisition and pair-bond formation (see section “Is floating a strategy or the ‘best of a bad job’?”), we define non-reproductives (NR) as adult birds that are temporarily or permanently excluded from the breeding pool. To be regarded as such, floaters must be present in breeding areas. Hence individuals that are alive but not present at breeding colonies are NR but should not be considered as floaters. Not all individuals in seabird populations experiencing ‘sabbaticals’ or breeding intermittently (e.g., Aebischer and Wanless, 1992) can be considered floaters as some may not be present at the breeding colonies. So not all NR are floaters nor are all floaters NR (see section “Is floating a strategy or the ‘best of a bad job’?”). Some studies have found that NR non-floaters are less common than NR-floaters (9% and 91% of NR, Harris and Wanless, 1995). Future long-term studies should attempt to separate the NR non-floater and floater categories. The discussion below deals with floaters irrespective of whether or not they are NR.

HOW ARE FLOATERS DETECTED?

Exhaustive individual marking and identification of all resident and transient birds is difficult but may enable a clear insight into the lives of floaters (Penteriani and Delgado, 2012). Non-invasive genetic techniques may offer a viable approach for detecting and estimating the abundance of floaters through sam-

pling of faeces or the feathers of moulting individuals (Rudnick *et al.*, 2008). The abundance of floaters can be inferred from the speed or frequency of mate replacement or territory reoccupation after the loss of an individual or a pair (Driscoll *et al.*, 1999; Fedy and Stutchbury, 2004; Schweizer and Whitmore, 2013; Mumme, 2015). There are also experimental ways to detect floaters. The rapid reoccupation of territories vacated through owner mortality may indicate the presence of numerous floaters (Vili *et al.*, 2013). The most common way with which floaters have been identified relies on experimental removal of territorial individuals and the detection of subsequent territory occupation by individuals not associated with any known territory or nest site. Newcomers should breed in the same year to confirm that they are mature and capable of breeding. Moreover, it is necessary that removal and replacement should involve both sexes as otherwise the experiment may reveal only an unequal sex ratio. A large fraction of avian studies incorporating floaters into the population picture have been based on experimental removals. Newton (1998) reviewed extensively the literature on removal experiments. From his table 4.1, one can deduce that one sex was replaced in 62% of 34 removal studies on 23 songbird species in spring, and in 23% both sexes were replaced. Replacements appeared in six of 12 studies of seven grouse species. For all species combined (74 studies on 53 species), there were replacements in 43%, indicating a non-breeder surplus.

The literature on replacement experiments for the last two decades (table 1) shows that 0-100% of removed males are replaced within periods ranging from a few hours to several weeks, with an average rate of replacement of $60\% \pm (\text{SD}) 34\%$ (13 studies on 11 species, table 1). Few studies have removed female territory owners (table 1) but they suggest that female floaters are less common ($43\% \pm 33\%$

replacement, $n = 6$ studies on six species). These data indicate that there are more male than female floaters (Marra and Holmes, 1997), although the difference between sexes in replacement rates is not significant (Mann-

Whitney U-test, $U = 31$, $P = 0.16$). They also show that male floaters can occupy a high proportion of vacancies, with replacements being more rapid and frequent in high quality, continuous habitats.

TABLE 1

Removal studies in which floaters have been detected (only involving reoccupation by floaters, not by neighbours or territory switchers).

[*Estudios de retirada de territoriales en que se han detectado flotantes (solo reocupación por flotantes, no vecinos o individuos que cambian de territorio.)*]

Species	Rate male replacement (n)	Rate female replacement (n)	Period	Reference
Bronze-winged jacana <i>Metopidius indicus</i>	33% (6)	33% (6)		Butchart <i>et al.</i> (1999)
Oystercatcher <i>Haematopus ostralegus</i>	61% (13)	53% (15)	15 days	Bruinzeel and van de Pol (2004)
Black redstart <i>Phoenicurus ochruros</i>	52% (23)		3 days	Villavicencio <i>et al.</i> (2013)
Eastern kingbird <i>Tyrannus tyrannus</i>	100% (3)	100% (3)	3 days	Cooper <i>et al.</i> (2009)
White-starred robin <i>Pogonocichla stellata</i>	43% in high quality habitat (7) 0% in low quality habitat (4)		2 days	Githiru <i>et al.</i> (2006)
White-bellied antbird <i>Myrmeciza longipes</i>	30% (10)	29% (7)	4 days	Fedy and Stutchbury (2004)
Red-shouldered widowbird <i>Euplectes axillaris</i>	100% (42) no full replacement		1 day	Pryke and Andersson (2003)
Ovenbird <i>Seiurus aurocapillus</i>	82% (11) in forest 20% (10) in fragment		10 days	Bayne and Hobson (2001)
Tree swallow <i>Tachycineta bicolor</i>	100% (12)		3 hours	Barber <i>et al.</i> (1998)
Black-tailed Blue warbler <i>Dendroica caerulescens</i>	100% (13)	0% (5)	1 day	Marra and Holmes (1997)
Dusky antbird <i>Cercomacra tyrannina</i>	56% (16)	42% (12)	14 days	Morton <i>et al.</i> (2000)

However, these studies offer only a partial view of the floating fraction as not all existing floaters may be able to occupy experimentally vacated territories. This has been shown for several species of forest grouse (Fischer and Keith, 1974; Lewis and Zwickel, 1980; Szuba and Bendell, 1988). The occupation of vacated territories may depend on territory quality, with floaters only colonising high quality areas (Manuwal, 1974; Bowman and Bird, 1986; Porter and Coulson, 1987; Newton and Marquiss, 1991; table 1). Some vacated territories may be occupied by neighbours and switching territory owners and not by floaters (Butchart *et al.*, 1999; Pryke and Andersson, 2003; Fedy and Stutchbury, 2004; Villavicencio *et al.*, 2013). Moreover, removal studies may only give a minimum estimate of floaters where 100% replacement occurs. The floater fraction can only be accurately estimated in these cases when the same number of territory owners as of existing floaters is removed. In removal studies on nest-box breeding populations, prompt occupation by presumed floaters has been detected after removal of nest-box owners (Heusmann and Belville, 1978; Alatalo *et al.*, 1983). The absence of replacements in some experiments where pairs or females are removed may be due to a lack of female floaters (Marra and Holmes, 1997).

In species that are limited by nest-site availability, such as many cavity-nesters, the provision of artificial sites such as nest-boxes often leads to an immediate increase in breeding density (Newton, 1994, 1998; Wiebe, 2011). Wiebe (2011) reviewed 31 studies of 20 species where the density of cavity nests in mature forest habitat was manipulated. Changes in breeding density on treatment plots were reported in ten experiments (32%), but statistically significant effects analysed by species were reported only in six cases (19%). With the exception of Bortolotti (1994), who added nest-boxes

late in the breeding season to test for the presence of floaters in the population, none of the studies attempted to determine whether NR occupied boxes. No researchers in studies in which changes in breeding density were found tracked the movements of individually marked birds before and after boxes were installed, and none estimated breeding densities in buffer zones surrounding the treatment plots to control for movements of individuals across plot boundaries. The conclusion by Wiebe (2011) is that reviewed studies provide no strong evidence that there is in fact a surplus of NR imposed by cavity limitation. Wiebe (2011) offers recommendations for the design of future studies wanting to approach this matter. However in some studies of non-forest birds, the occupation by floaters was confirmed through rings (Stutchbury and Robertson, 1985; Village, 1990). Saitou (2001) put up additional nest-boxes for grey starlings *Sturnus cineraceus* and these were quickly occupied by floaters in the early part of the breeding season. The intensity of intraspecific brood parasitism (IBP) was significantly reduced. The removal of boxes had the opposite effect. Floater females were thus involved in IBP before manipulation. As in removal experiments, the possibility that newcomers arrive from breeding territories elsewhere should be excluded before a rise in breeding density can be attributed to the presence of floaters. Moreover, as in removal experiments, the numbers of floaters may be underestimated.

Another form of floater detection has involved studies on extra-pair paternity in populations of genotyped territorial birds. Commonly in these studies, the sires of many extra-pair offspring are not identified genetically among territorial genotyped males (table 2). In general, almost two-thirds of extra-pair offspring ($64 \pm 20\%$, $n = 7$ studies on 6 species) in recent studies of extra-pair paternity are not assigned to a sire among resident territorial males (table 2). This frac-

tion may be overestimated if some territorial males escape control by researchers. The options are that these sires are male floaters or that they are territorials outside the study area (Peer *et al.*, 2000; Kempnaers *et al.*, 2001). Given that the first possibility appears

more plausible based on the presumed costs of looking for extra-pair copulations (EPCs) far from the territory (Dunn *et al.*, 1994; but see Leisler *et al.*, 2000; Kempnaers *et al.*, 2001), the evidence of floater existence derived from extra-pair paternity studies

TABLE 2

Proportion of extra-pair young (EPY) sired by floater males (*, considering broods with genetically identified floaters) or by unidentified males not recorded as territorial (no floaters identified as such), and the proportion of broods containing some EPY. The numbers of nestlings and broods studied are also presented.

[Proporción de pollos extrapareja (EPY) producidos por machos flotantes (*, considerando nidadas con flotantes identificados genéticamente) o por machos no identificados y no registrados como territoriales (sin flotantes identificados como tales), y la proporción de nidadas con algún EPY. Se presentan también las cifras de pollos y nidadas estudiados.]

Species	Proportion EPY with non-resident sire(n)	Proportion broods with EPY with non-resident sire(n)	Broods (nestlings) studied	Reference
Cooper's hawk <i>Accipiter cooperii</i>	89% (27)	87% (15)	44 (140)	Rosenfield <i>et al.</i> (2015)
Eastern kingbird <i>Tyrannus tyrannus</i> *	5% (63)		53 (116)	Cooper <i>et al.</i> (2009)
Pied flycatcher <i>Ficedula hypoleuca</i>	46% (35) 65% (55)	59% (17) 61% (23)	59 (268) 60 (313)	Moreno <i>et al.</i> (2013) Moreno <i>et al.</i> (2015)
White-throated magpie-jay <i>Calocitta formosa</i> *	33% (84)	15% (23)	32 (110)	Berg (2005)
Tree swallow <i>Tachycineta bicolor</i> *	20% (35) 79% (117) 79% (63)	10% (13) 89% (36) 75% (20)	21 (104) 49 (229) 23 (119)	Kempnaers <i>et al.</i> (2001) Kempnaers <i>et al.</i> (1999) Dunn <i>et al.</i> (1994)
Great reed warbler <i>Acrocephalus arundinaceus</i>	53% (19)	60% (5)	48 (194)	Leisler <i>et al.</i> (2000)
Stitchbird <i>Notiomystis cincta</i> *	42% (12)	37% (8)	10 (34)	Ewen <i>et al.</i> (1999)
Orange-tufted sunbird <i>Nectarinia osea</i> *	13% (8)	12% (8)	47 (88)	Zilberman <i>et al.</i> (1999)
Great-tailed grackle <i>Quiscalus mexicanus</i>	36% (44)		(120)	Johnson <i>et al.</i> (2000)

appears robust. The same can be said for genetically identified cases of IBP where the parasitic embryos or nestlings cannot be genetically connected with any identified breeding female in the study area. These cases appear much less frequently, which may signify that in most populations female floaters constitute a relatively smaller fraction than male floaters. In studies in which the floater fraction has been genetically identified, one in four extra-pair offspring are sired by identified floaters ($23 \pm 15\%$, $n = 5$ studies on 5 species, table 2). The lower rate of floater involvement recorded in these studies compared with participation in extra-pair activity by unidentified males may be due to incomplete floater identification or to incomplete monitoring of territorial residents in the studies mentioned above. Alternatively, unidentified sires may be resident in unmonitored adjacent habitats. In any case, these studies imply scant reproductive success for the fraction of floaters involved in EPC, thereby strengthening the ‘best of a bad job’ hypothesis (see section “Is floating a strategy or the ‘best of a bad job’?”). The main fraction of floaters may not reproduce at all (Cooper *et al.*, 2009).

Some studies have identified floaters through territory take-overs after nest-building and egg-laying (Butchart *et al.*, 1999; Moreno, 2015) or during repeated visits to leks (Westcott and Smith, 1994). The birds taking over territories at this stage may induce floater or NR status in the evicted individuals, which have no time to establish a territory of their own or to form a pair bond (Piper *et al.*, 2000; Fedy and Stutchbury, 2004). However, the possibility remains that evicted birds are successful in establishing themselves away from the study area where the take-over took place and thus remain undetected as late territorials.

Acoustic marking (Voegeli *et al.*, 2008; Kirschel *et al.*, 2011) and recordings of spontaneous calls together with broadcast

of male territorial songs in owls (Martínez and Zuberogoitia, 2002) have also been useful in detecting floaters. Estimates of numbers of floaters based on visual estimation may seriously underestimate their frequency when compared with non-invasive genetic sampling (Katzner *et al.*, 2011).

HOW LARGE IS THE FLOATER AND NR FRACTION?

If floaters and NR constitute very small fractions of avian populations, their role in clarifying the strength of sexual selection may be irrelevant. Therefore, it is essential to know the size of the pool of floaters and NR in any populations for the purposes of this review. The traditional focus of the literature on avian floaters is on the importance of density-dependent population regulation. Territoriality is described as a process regulating population numbers by excluding certain individuals from breeding when density approaches a critical level (Newton, 1998). The argument involved occasionally a group-selection aspect, now discredited, portraying reproductive exclusion as an adaptation for promoting higher success for the population as a whole (Wynne-Edwards, 1962). However, group selection is unnecessary in this context as individuals may achieve the exclusion of others through their own competitive behaviour that is favoured by individual selection (Newton, 1998). The emphasis has been put on food resources as the main driver of the size of any population. Individuals are excluded from breeding by territorial birds wanting to ensure sufficient food resources for breeding successfully. This argument does not apply to colonial birds whose territories only include a small area around their nest site without any food resources. Nevertheless, there also floaters in colonial seabird populations (Young, 1972; Manuwal, 1974; Pierotti, 1980). Thus exclu-

sion seems to involve something else than just food supplying territories. Reproductive exclusion is directly related to the capacity to acquire mates or space for breeding in competitive contexts. Stronger limitations on these resources are likely to result in a larger floating or NR population.

It has been assumed that floaters constitute a larger fraction of the population in large long-lived birds, given the existence of a large pool of young, immature birds and the occurrence of delayed breeding in these species (Newton, 1998). However, if we exclude the immature fraction from the non-breeding pool, the contention remains questionable. It could be based on the difficulty of observing and counting floaters in small, short-lived species. Brown (1969) estimated a theoretical maximum ratio of non-breeders to breeders for a range of bird species with different reproductive and mortality rates. In the most extreme case, non-breeders could outnumber breeders by two or more times. Thus, in theory, competition for breeding resources (including participation in leks) could be excluding a large fraction of individuals from reproduction.

The literature shows that floaters may represent in fact a considerable fraction of the population for both sexes. Newton (1998) reviewed published papers up to 1996. Based on his table 3.2, we may conclude that in 20 studies on 17 species, ranging in size from wrens to swans, on average $39\% \pm 22\%$ (range 3%-72%) of individuals were non-territorial non-breeders. In eight studies in which fractions were estimated separately for both sexes, the value was higher for males in six cases and higher for females in two cases. Values for females ranged from 0 in the song sparrow *Melospiza melodia* to 62 in the northern goshawk *Accipiter gentilis* (mean $28\% \pm 26\%$, $n = 10$ studies). This indicates that, although less common than male floaters, female floaters are present in some avian populations and may constitute

an important fraction of females. Although values are generally higher for large species in Newton's review, they may include immature birds which are not dealt with here. It is therefore possible that mature non-breeders are as common in large-bodied as in small-bodied species.

Studies from the last two decades in which the floater fraction has been identified, and some papers not cited by Newton (1998), show that $41\% \pm 26\%$ of individuals behave as floaters (eight studies on seven species) (table 3). In studies in which the floater fraction has been estimated separately for the two sexes, $40\% \pm 23\%$ of males (14 studies on 14 species) and $23\% \pm 18\%$ of females (nine studies on nine species) behave as floaters (table 3). Again, we find that female floaters are less abundant in avian populations than male floaters, although the difference is not quite significant (Mann-Whitney U-test, $U = 33$, $P = 0.058$). However, floaters may still represent a considerable fraction of individuals even for females. These figures do not change appreciably if we exclude studies in which it is specified that the floater fraction includes juveniles (table 3). Unfortunately, most studies do not report the proportion of floaters made up of juveniles. The fact that between a quarter to almost half of the population in these studies is made up of non-territorial floaters supports the importance of considering this fraction in studies on sexual selection.

ARE FLOATERS PHENOTYPICALLY DIFFERENT FROM RESIDENTS?

Excluding situations in which it is predominantly young birds that are prevented from breeding, it would be interesting to know the traits characterising floaters when compared to territorials and the factors that may facilitate the transition between floater and territorial status. In some long-lived

TABLE 3

Presence (Y = yes, N = no) and fractions of floaters (number of individuals in parenthesis) in avian populations (ads includes specifically only non-juveniles, juv includes young birds that reproduce later, m&f presents joint data for both sexes, when several years are presented averages or data for the year with most data are given).

[Presencia (Y = si, N = no) y fracciones de flotantes (número de individuos en paréntesis) en poblaciones de aves (ads incluye específicamente solo no juveniles, juv incluye jóvenes que se reproducen luego, m&f presenta datos para el conjunto de los dos sexos, cuando se presentan varios años se ofrecen medias o datos del año con más datos).]

Species	Presence of male floaters	Fraction of male floaters	Presence of female floaters	Fraction of female floaters	Reference
Short-tailed shearwater <i>Puffinus tenuirostris</i>	Y ads	18% (long-term average)	Y ads	14% (long-term average)	Bradley <i>et al.</i> (2000)
Imperial eagle <i>Aquila heliaca</i>	Y m&f	82% (376)			Katzner <i>et al.</i> (2011)
Bearded vulture <i>Gypaetus barbatus</i>	Y m&f	22% (227)			Gómez de Segura (2012)
	Y m&f	39% (38)			Antor <i>et al.</i> (2007)
Great-horned owl <i>Bubo virginianus</i>	Y m&f	29% (28)			Rohner (1997)
Common guillemot <i>Uria aalge</i>	Y ads	7.6% (171)	Y	6.4% (157)	Harris and Wanless (1995)
Aldabra rail <i>Dryolimnas aldabranus</i>	Y m&f	36% (10900)			Hockey <i>et al.</i> (2011)
Waffled jacana <i>Jacana jacana</i>	Y	40% (252)	Y	39% (139)	Emlen and Wrege (2004)
Bronze-winged jacana <i>Metopidius indicus</i>	Y	55% (40)	Y	50% (22)	Butchart (2000)
Hoopoe <i>Upupa epops</i>	Y juv	22% (18)			Gruell <i>et al.</i> (2007)
Slate-throated redstart <i>Myioborus miniatus</i>	Y juv	67% (6)	N		Mumme (2015)
Mexican ant-thrush <i>Formicarius moniliger</i>			Y	37% (19)	Kirschel <i>et al.</i> (2011)
Red-billed cough <i>Pyrhocorax pyrrhocorax</i>	Y m&f	64% (2614)			Blanco <i>et al.</i> (2009)
Eastern kingbird <i>Tyrannus tyrannus</i>	Y juv m&f	57% (83)			Cooper <i>et al.</i> (2009)

TABLE 3 (cont.)

Species	Presence of male floaters	Fraction of male floaters	Presence of female floaters	Fraction of female floaters	Reference
Canada warbler <i>Wilsonia canadensis</i>	Y ads	7% (41)			Reitsma <i>et al.</i> (2008)
Grey-crowned babbler <i>Pomatostomus temporalis</i>	N m&f				Eguchi <i>et al.</i> (2007)
White-starred robin <i>Pogonocichla stellata</i>	Y	48% (37)	Y	7% (15)	Githiru <i>et al.</i> (2006)
White-bellied antbird <i>Myrmeciza longipes</i>	Y	16% (57)	Y	17% (41)	Fedy and Stutchbury (2004)
Red-shouldered bishop <i>Euplectes axillaris</i>	Y	55% (118)			Pryke and Andersson (2003)
Grey starling <i>Sturnus cineraceus</i>	Y	73% (30)	N	0% (18)	Saitou (2001)
Great-tailed grackle <i>Quiscalus mexicanus</i>	Y	72% (29)			Johnson <i>et al.</i> (2000)
Dusky antbird <i>Cercomacra tyrannina</i>	Y	33% (9)	Y	40% (5)	Morton <i>et al.</i> (2000)
Ochre-bellied flycatcher <i>Mionectes oleaginosus</i>	Y	48% (73)			Westcott and Smith (1994)

birds, site tenacity appears to be more important than age in determining an individual's success in establishing a territory (Sergio *et al.*, 2009; Loewenthal *et al.*, 2015). Some studies have shown that floaters were drawn from among the most dominant individuals in the non-territorial fraction of the population (Knapton and Krebs, 1974; Smith and Arcese, 1989). In several studies in which removed territory owners were held captive and later released, such birds mostly managed to displace their replacements to regain their territories and mates, either in the same year or the next (Watson and Jenkins, 1968; Harris, 1970; Smith, 1978; Szuba and Bendell, 1988; Village, 1990). This indicates

that replacing floaters are subdominant to the original territory owners. In the great tit *Parus major*, however, the probability that replacement pairs would be able to retain their territories increased with the time elapsed before the original owners were encountered again, supporting a role for 'owner' effects (Krebs, 1982). Size or condition is often linked to non-territorial status (Alisauskas, 1987; Richner, 1989). A defining characteristic of floaters in migratory species may be delayed arrival at the breeding grounds (Sergio *et al.*, 2009). However, delayed arrival is probably the consequence of certain physiological or behavioural attributes, so future studies should clarify the underlying basis for late

TABLE 4

Phenotypic differences (= similar, > < different, > greater, < smaller) between floaters (F) and territorials (T) and method used for the identification of floaters (R = removal, B = Banding and territory mapping).

[*Diferencias fenotípicas (= similar, >< diferente, > mayor, < menor) entre flotantes (F) y territoriales (T) e identificación de flotantes (R = retirada, B = marcaje y mapeo de territorios).*]

Species	Traits analyzed	Trend	Sex	Identification	Reference
Black kite <i>Milvus migrans</i>	Circulating carotenoids	F < T	M	B	Blas <i>et al.</i> (2013)
		F = T	F		
	Ornament expression	F < T	M, F	B	Blas <i>et al.</i> (2011)
		F = T	M, F		
		F > T	M		
	Testosterone level	F < T	F	B	Blas and Hiraldo (2010)
		F = T	M		
F < T		F			
F = T		M			
Estradiol level	F < T	F	B	Blas and Hiraldo (2010)	
	F = T	M			
	F < T	F			
Progesterone level	F < T	F	B	Blas and Hiraldo (2010)	
	F = T	M			
	F < T	F			
Waffled jacana <i>Jacana jacana</i>	Size, mass	F < T	M, F	B	Emlen and Wrege (2004)
	Ornament size	F < T	M, F		
	Ornament expression	F < T	M, F		
Bronze-winged jacana <i>Metopidius indicus</i>	Mass	F < T	M, F	B	Butchart (2000)
	Condition	F = T	M		
		F < T	F		
	Ornament size	F < T	M		
Inca tern <i>Larosterna inca</i>	Ornament size	F < T	M, F	B	Velando <i>et al.</i> (2001)
		F = T	F		
Wire-tailed manakin <i>Pipra filicauda</i>	Testosterone level	F < T	M	B	Ryder <i>et al.</i> (2011)
White-bellied antbird <i>Myrmeciza longipes</i>	Condition	F = T	M, F	B	Fedy and Stutchbury (2004)
Red-shouldered bishop <i>Euplectes axillaris</i>	Size, condition	F = T	M	B	Pryke and Andersson (2003)
	Ornament size, hue	F < T	M		
	Dominance at feeder	F < T	M		
Black redstart <i>Phoenicurus ochruros</i>	Condition	F > T	M	B	Andersson (1994)
	Testosterone level	F = T	M		
Black redstart <i>Phoenicurus ochruros</i>	Testosterone level	F = T	M	R	Villavicencio <i>et al.</i> (2013)
	Aggressive behaviour	F = T	M		

TABLE 4 (cont.)

Species	Traits analyzed	Trend	Sex	Identification	Reference
Red-winged blackbird <i>Agelaius phoeniceus</i>	Size, mass, condition	F = T	M	R	Shutler and Weatherhead (1991)
	Ornament size	F = T	M		
Tree swallow <i>Tachycineta bicolor</i>	Mass, condition	F > T	M	B	Kempnaers <i>et al.</i> (2001)
	Cloacal protuberance	F > T	M	B	Peer <i>et al.</i> (2000)
	Sperm no. during copul. per.	F > T	M		
	Testes mass	F = T	M		
	Size, mass, condition	F = T	M	B	
	Size, mass	F = T	M	R	Barber <i>et al.</i> (1998)
	Wing length	F < T			
Great-tailed grackle <i>Quiscalus mexicanus</i>	Mass	F < T	M	B	Johnson <i>et al.</i> (2000)
	Ornament size	F < T	M		
European starling <i>Sturnus vulgaris</i>	Size, mass	F < T	F	B	Sandell and Diener (1999)

initiation of migration or migration speed, although delayed arrival must sometimes be due to extrinsic factors, notably weather. Breeders and floaters may also show a different habitat use (Campioni *et al.*, 2010, 2012) and diet (Caro *et al.*, 2011). These differences may be a consequence, not the source, of floater status.

Excluding age, several other traits have been related to floater status. I have revised the literature for the last two decades for studies in which an attempt has been made to compare traits of territory occupants and floaters (table 4). Studies that clearly confound floaters with dispersing juveniles have not been included here. These studies present a mixed picture in which floaters do not differ from residents at all or only with respect to specific traits (table 3). The most common traits analysed are mass and body condition (ten studies on eight species), structural body size (six studies on five species) and ornament size (seven studies on seven species).

Floaters are lighter in three cases and smaller in two cases, with two studies showing floaters in better condition than residents. Thus, there is no clear evidence that either size or condition is necessary for explaining floater status generally. However, in six of seven studies (86%) male floaters were less ornamented than residents and in three of four cases (75%) female floaters were less ornamented. Thus, the literature suggests that ornament size and expression are involved in territorial exclusion and may be either its cause or one of its consequences. Experiments in which ornament expression is manipulated and its consequences for acquisition of floater status evaluated are sorely needed. Testosterone levels have been measured in four studies on three species (table 4) and were lower in floaters than in resident territorials in only one case. Floaters proved to be less aggressive in only one of two studies on dominance and aggression. Thus, testosterone does not seem to be involved in

determining floater status, although data are scant. One conclusion from this review is that excluding floaters from an analysis of sexually selected traits may severely bias distributions towards larger ornament sizes or more intense expressions.

IS FLOATING A VIABLE STRATEGY OR THE 'BEST OF A BAD JOB'?

There is evidence that floaters survive less well than territorials, and that changes in territorial status are accompanied by changes in survival rates (e.g., Carrick, 1963; Smith, 1976; Watson, 1985; Harris and Wanless, 1995; Rohner, 1995; Cam *et al.*, 1998; Dwyer *et al.*, 2012). Together with the reduction in breeding opportunities (Smith and Arcese, 1989; Stutchbury and Robertson, 1985, 1987) this supports the contention that floaters are low-quality birds following a conditional strategy that, in general, implies reduced fitness (Newton, 1998). In several species, replacers achieve significantly lower reproductive success than the original territorial occupants, a probable effect of their younger age (Manuval, 1974; Village, 1990; Newton and Marquiss, 1991; Komdeur and Edelaar, 2001). The evidence on breeding performance excluding age effects is scant (Linz *et al.*, 2011). Intermittent breeding in seabirds may be an indication of poor ability to raise progeny (Bradley *et al.*, 2000). However, there is some evidence that certain male floaters may obtain some reproductive success through extra-pair copulations (EPC) (Ewen *et al.*, 1999; Johnson *et al.*, 2000; Leisler *et al.*, 2000; Peer *et al.*, 2000; Conrad *et al.*, 2001; Kempnaers *et al.*, 2001; table 2). In some cases, floaters enjoy a better body condition than territory owners (Andersson, 1994; Kempnaers *et al.*, 2001) which could allow them to pursue EPC successfully. Floating may also constitute a temporary conditional strategy in some cases (Fedy and

Stutchbury, 2004). The possibility that floating may constitute a successful alternative strategy in some species, as shown for 'sneaker' strategies in some fish (Taborsky, 1994), remains a tantalising possibility to be explored. However, it should be shown that floaters on average and not just in a fraction of cases attain similar lifetime fitness as territory owners on average. For that, we require data on survival and lifetime reproduction of most of the floaters in a population.

Although there is some disagreement concerning the relative success of these floater strategies compared with territorial ones, the preliminary consensus at present, based on as yet scant studies, is that floaters are 'making the best of a bad job' (Rohner, 1995, 1997; Newton, 1998; Cam *et al.*, 1998; Johnson *et al.*, 2000; Cooper *et al.*, 2009). Thus, although adult male floaters appear capable of engaging in extra-pair copulations in the red-winged blackbird *Agelaius phoeniceus* (Moulton *et al.*, 2013), no direct genetic evidence exists to indicate that they produce extra-pair young (Weatherhead and Boag, 1995; Gray, 1996; Yasukawa *et al.*, 2009). In fact, male floaters appear to be waiting in most cases for 'real' reproductive options through territory acquisition (Smith, 1978; Ens *et al.*, 1995; Bruinzeel and van de Pool, 2004), something unexpected if floating is a stable evolutionary strategy. Involuntary movement between nest sites or territories may be followed by floating during several years (Kokko *et al.*, 2004), which suggests that floating is also involuntary. Moreover, floaters have to compete with territorial individuals, who may be responsible for most extra-pair affairs (Zilberman *et al.*, 1999; table 2). The general pattern is for territorial males to sire the majority of offspring (Jonson *et al.*, 2000).

Female floaters could compensate for their lack of pair bonding and territoriality through intense egg dumping (Sandell and Diemer, 1999; Saitou, 2001). Parasitic females have

been shown to be of high quality and to survive better in the cliff swallow *Petrochelidon pyrrhonota* (Brown and Brown, 2004). However, full compensation of their floater status would probably require intensities of IBP only found in some species (Zhang *et al.*, 2011). Moreover, there is evidence that intraspecific egg dumping in ducks is in fact mediated through kin selection (Andersson, 2001). The evolutionary stability of alternative reproductive strategies in birds is therefore not ensured. However, the possibility of floating as a successful strategy remains suggestive.

LIMITATIONS ON REPRODUCTIVE RESOURCE ACQUISITION

Shortages of mates or breeding space may involve skewed population sex ratios, polygamous mating systems, high population densities and specific breeding requirements such as space in colonies or adequate nesting cavities. Population density is thus only one factor promoting the existence of floaters and NR. Some studies have linked reproductive exclusion of males in monogamous systems to a scarcity of females in the population induced by ecological factors. Females may be more vulnerable to several mortality factors, such as starvation or predation on the nest (Breitwisch, 1989). However, the population sex ratio is frequently deduced from the territorial fraction of the population without considering the floater fraction. Nevertheless, there may be a considerable fraction of female floaters excluded from reproduction due to lack of mates or resources, whose inclusion could change the sex ratio estimates derived by researchers. Until this fraction is included in sex ratio computations, the sex ratio basis for male floating remains in doubt.

The opportunity for sexual selection has frequently been linked to operational sex

ratios. The operational sex ratio (OSR) is usually defined as the ratio of fertilisable females to sexually active males and its derivation in practice excludes individuals whose status is either unknown or uncertain regarding their capacity to reproduce. The ratio of male to female floaters may be different from the OSR and may have consequences for sexual selection. A strong bias towards male floaters may promote competitive behaviours in males while the opposite bias would favour female signalling and competition. The mating system may critically impinge on the sex ratio of the floater population. In strongly polygynous systems, many males are necessarily excluded from reproduction (Shutler and Weatherhead, 1991, 1994; Moulton *et al.*, 2013), while the opposite may happen in socially polyandrous systems (Butchart, 2000; Emlen and Wrege, 2004). Given an unbiased population sex ratio, we should expect more male than female floaters in the former case and the opposite in the latter. The degree of polygamy may thus constitute a critical factor in explaining the frequency of floaters in avian populations. Floating is thus a product of sexual selection that may in turn promote further sexual selection to evade this fate in a vicious circle, whose evolutionary outcome we can observe today.

The main cause of floating has traditionally been considered to be habitat crowding in conjunction with territoriality (Newton, 1998). Accordingly, habitat limitation should promote floating (Komdeur, 1996; Snetsinger *et al.*, 2005). Rigid territoriality and high life expectancy may induce floater behaviour depending on prey density (Barraquand *et al.*, 2014). Even in lekking species, opportunities for acquiring territories may be limited (Ryder *et al.*, 2011). Many colonial birds are restricted to breeding at specific locations with adequate conditions with respect to predator avoidance, ease of access or proximity to food sources. Adequate space

or nest sites could be as limiting in colonial species as in those with food-based territories. We should expect considerable floater fractions in species with the most restricted habitat requirements for breeding (reviewed in Newton, 2008). Other birds require cavities for nesting that they cannot excavate themselves (secondary cavity nesters). Access to these cavities when in short supply may be limited and may exclude a fraction of potential breeders from reproduction (Newton, 1994, 1998; Wiebe, 2011). We should expect a higher floater fraction in cavity nesters than in open nesters in otherwise similar conditions i.e. within the same study area. To my knowledge, no study has approached this issue with marked floaters. There is evidence that floaters prefer to wait for vacancies in good breeding areas rather than occupying low quality areas (Manuwal, 1974; Lewis and Zwickel, 1980; Porter and Coulson, 1987; Newton and Marquiss, 1991; Rutz and Biljsma, 2006). They may also confront the choice of accepting a poor territory now or waiting another year or years before a better territory becomes available (Ens *et al.*, 1995; Holt and Martin, 1997). Floaters may in effect be queuing for good territories (Smith, 1978; Bruinzeel *et al.*, 2006). Thus, competition for good sites may be determining the size of the floater fraction. Without good knowledge of the determinants of habitat quality for breeding, the presence of a considerable fraction of floaters may be difficult to understand.

EXCLUSION: TEMPORARY OR PERMANENT?

Few studies have been able to clarify the duration of floater status in any population. Floaters may either acquire a territory or disappear without breeding (Piper *et al.*, 2000; Piper, 2001). Evicted territory owners may become floaters that may later return to resident status (Westcott and Smith, 1994;

Butchart, 2000). Temporary floater status may not imply permanent exclusion from the breeding pool in long-lived birds (Saitou, 2001; Fedy and Stutchbury, 2004; Schmutz *et al.*, 2014). Thus, so-called 'sabbaticals' or extended non-breeding periods are common in seabirds and may only involve temporary floater status (Aebischer and Wanless, 1992; Bradley *et al.*, 2000). However, being a floater in one year may significantly reduce the chances of breeding the next year (Cam *et al.*, 1998). Site tenacity may contribute to success in establishing a territory rather than age *per se* (Loewenthal *et al.*, 2015). For short-lived species, NR status in a single breeding season may in fact imply zero lifetime reproductive success. Thus there should be stronger selection for avoiding floater status in short-lived birds. This should be expressed through the extent and intensity of aggressive territory take-over behaviour in both males and females of these species. Lethal levels of aggression have been observed in passerines in contexts of territory take-overs by females (Moreno, 2015). Strikingly little is known on the levels of lethal intraspecific aggression and the frequency of deaths in either sex in territorial or mate-acquisition contexts. Deaths during competition for reproductive resources may be the expression of selection for avoidance of floater status.

The literature on NR in social species is covered under the term "reproductive skew". When not linked to age-dependent processes, NR in avian social groups experience the same fitness reduction as in other species (Stacey and Koenig, 1990; Ridley *et al.*, 2008). Avian sociality may be favoured by the costs of living alone as a floater in social species (Ridley *et al.*, 2008), but may be constrained by adaptations for avoidance of NR status. The absence of any floaters has been detected in at least one species of cooperative breeder (Eguchi *et al.*, 2007), which may suggest that floaters become

subordinate helpers in these species in order to avoid permanent exclusion from breeding resources. The increased aggressiveness promoted by NR may inflate the costs of coexisting in social groups and favour solitary living or family groups where kin selection may soften competition for breeder status to some degree. Although reproductive skew has received a great deal of attention recently, it has not been clearly linked to studies on floaters in avian populations. It is doubtful if any social grouping can sustain permanent exclusion of breeding status in some of its members without breaking apart. We should not therefore expect drastic and permanent measures of reproductive exclusion affecting adult birds in group-living birds.

COMPETITION OR CHOICE?

Since Darwin (1871), the two main mechanisms behind sexual selection are considered to be competition for reproductive resources and choice by the operationally limiting sex, usually females. In males, the existence of a considerable fraction of NR attempting to breed may select for intense territorial behaviour and competitive mate guarding tactics in territory holders and in aggressive territory acquisition tactics in floaters (Arcese, 1987; Westcott and Smith, 1994; Zilberman *et al.*, 2001; Carmen, 2004; Gruell *et al.*, 2007; Moulton *et al.*, 2013; Turrin and Watts, 2014). A higher density of floaters may require a higher level of signalling in territory owners throughout the season (Stutchbury, 1992; Sunde and Bolstad, 2004; Penteriani and Delgado, 2008). Floaters may prospect for territorial vacancies intensively, explaining the frequent appearance of intruder males at active nests (Tobler and Smith, 2004; Dwyer *et al.*, 2013; Veiga *et al.*, 2013; Turrin and Watts, 2014; Wischhoff *et al.*, 2015). They may look out for weak or senes-

cent territory owners (Westcott and Smith, 1994; Bornschein *et al.*, 2015). Only high quality owners may be able to keep away intruders (Moreno *et al.*, 2013). Increasing interference competition from floaters may explain why some territories experience a density-dependent reduction in reproductive success (Bretagnolle *et al.*, 2008; Grunkorn *et al.*, 2014). Floater pressure may impose the formation of polyandrous trios in some cases (Carrete *et al.*, 2006). Floaters may use the presence of nestlings or fledglings to target territories for future attempt at territorial take-over (Piper *et al.*, 2006). The high level of male-male aggression (Sunde and Bolstad, 2004) and of attacks on chicks by floaters (Kazama *et al.*, 2012) observed in some populations may be difficult to understand without considering the need to obtain a territory and such behaviour may compromise the reproductive success of the breeding fraction (e.g., Carrete *et al.*, 2006; Kazama *et al.*, 2012).

Floater males may be also selected to try to force copulations or harass females in relentless attempts to reproduce (Moulton *et al.*, 2013). Females may obtain direct benefits from mating with dominant males that can keep harassing floaters away (Moreno *et al.*, 2013). The existence of intense male aggression towards other males, and towards breeding females, may be the consequence of the existence of a considerable floater fraction. Only aggressive floaters in the past may have contributed genes to future generations. Females may have been selected to avoid male harassment and forced copulations, which may explain the rarity of extra-pair fertilisations in many studies – most workers explain this rarity by female choice mechanisms. More work is required to clarify the importance of floaters in the evolution of extra-pair paternity.

In females also, the desperate attempts by floaters to attain breeding opportunities may have contributed to the observed propensi-

ties for prospecting by females (Veiga *et al.*, 2013) and for female-female aggression and the signalling of female dominance towards other females (Stutchbury and Robertson, 1987; Moreno *et al.*, 2014). Female floaters may frequently be chased away by territory owners to preclude IBP tactics (Veiga *et al.*, 2012) and this may lead to increased androgen levels in females in high density situations with the presence of more floaters (Pilz and Smith, 2004). The need to avoid such aggression may have selected for delayed plumage maturation in females of some species (Coady and Dawson, 2013). Although female aggression towards other females has received much less attention than male aggression, evidence is accumulating that females may compete aggressively for breeding opportunities and that they may signal their aggressive dispositions (Tobias *et al.*, 2012; Cain and Rosvall, 2014). Including avoidance of NR status in analyses may help to explain the current distribution of social signals during the breeding season in female birds.

Floater males may try to attract fertile females for EPCs by exhibiting signals of quality (Gruell *et al.*, 2007). Given the low social status of floaters observed in several studies (see below), their success in this endeavour appears doubtful (Moulton *et al.*, 2013). Some studies report a high proportion of unidentified EPC perpetrators which suggests that EPCs may be driven to a large extent by floater activity (see above). The relative importance of extra-pair female mate choice versus male drive to obtain EPCs at any cost is currently under debate. Under the first scenario, females could be attempting to ameliorate their initial pair choice concerning social bonds by seeking EPCs. Including floaters in this scenario of female choice is the unavoidable consequence of the presence of floaters among extra-pair sires. However, it is at present risky to assume that all floater-dependent EPCs rely

on female mate choice. The aggressive scenario of male harassment and forced copulation attempts remains a plausible alternative (Westneat and Stewart, 2003).

In the case of female floaters, they may be less attractive to territorial males and thereby receive less male support in competitive interactions. This possibility has not been well covered by the literature, although there is evidence that females are more aggressive towards intruders when mates are absent and when mates have low testosterone levels (Morales *et al.*, 2014; Moreno *et al.*, 2015). These results suggest that females rely partly on their mates to conserve their mating status. Being attractive may strengthen mate support in territorial contests with intruding female floaters. Thus, there may exist selection in females for signalling quality to mates in order to avoid being evicted and converted into female floaters. Female floaters may be more prone to intrude in occupied territories than male floaters due to the lower risk of suffering attacks by male owners (Campioni *et al.*, 2010).

THE UNDERESTIMATION OF SEXUAL SELECTION

Relating the mating and reproductive success of territorial birds to the expression of potential signals or weapons is the typical approach of studies on sexual selection. Expression of sexually selected traits can be experimentally manipulated or just observed in natural conditions. In studies excluding floaters, trait expression by the NR fraction of the population is unknown. Therefore, the full population range of variation of the traits studied is insufficiently understood (see above). Existing trait expression in the territorial fraction may be difficult to interpret without considering the range of values removed by selection acting on floaters (fig. 1). Current selection acting on certain

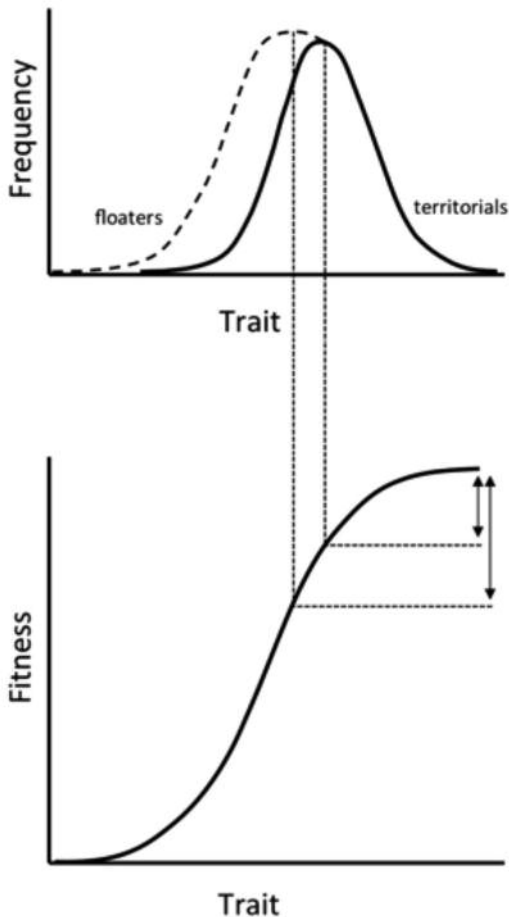


FIG. 1.—Upper graph: Including floaters (broken line) may displace the distribution of a sexually selected trait towards lower expressions than observed in territorials (continuous line). Lower graph: This implies that the fitness difference between maximum and mean values (dotted lines) is greater when floaters are included in the study and selection is accordingly stronger (arrows).

[Gráfico superior: Incluir a los flotantes (línea a trazos) puede desplazar la distribución de rasgos sexualmente seleccionados hacia expresiones más bajas que lo observado en los individuos territoriales (línea continua). Gráfico inferior: Ello implica que las diferencias en eficacia biológica entre los valores máximo y medio (líneas punteadas) es mayor cuando se incluye a los flotantes en el estudio y la selección correspondientemente más fuerte (flechas).]

traits may be underestimated when the fraction of individuals with low reproductive success imposed by floater status is excluded from the analyses (fig. 1). The importance of sexual selection may be negated when, in fact, its action on floaters may be maintaining current levels of trait expression in the territorial fraction. Phenotypic variation in the breeding population may be unrelated to mating or breeding success but its existence may be explained by selection against unidentified phenotypes in the coexisting floater population. We should be therefore remiss to disclaim sexual selection processes operating in populations when the floater fraction has not been identified. Studies estimating sexual selection differentials with and without including floaters should be conducted to judge the degree of underestimation of sexual selection in the literature.

The existence of female floaters raises the question of determinants of the strength of sexual selection forces. If these females could breed, the OSR would be less male-biased and thereby could soften inter-male competition for breeding opportunities. Thus, egg dumping apart, the exclusion of certain females from the reproductive fraction should be studied as a driver of sexual selection whose importance depends on the fraction of NR females. The extent of female floating should depend on female competition for reproductive resources which prevents males from attracting other females to their territories and determines the lower limits on territory size. These processes, considered by some authors to be covered by the term 'social selection' but here included in a wide conception of sexual selection, may be essential in explaining the expression of territorial behaviour, aggression and signalling in birds, as well as in other animals. Female-female competition for breeding resources may be limiting the female breeding pool and inducing strong competitiveness and attractiveness in males to ensure their

breeding status. The existence of floaters confirms the vital role of female competitiveness in driving sexual selection.

An assumption in population biology and conservation biology is that floaters constitute a buffer that may dampen increases in breeder mortality, thereby reducing the extinction risk of populations (Newton, 1998; Sarah *et al.*, 2004; Blanco *et al.*, 2009; Penteriani *et al.*, 2011; Hockey *et al.*, 2011). This assumption is based on the supposed

phenotypic similarity of breeder and floater fractions, possibly only separated by age (Penteriani *et al.*, 2009). However, the substitution of competitively superior, high-quality breeders by floaters may in fact represent a decline in the mean phenotypic quality of breeders, based on available evidence on non-juvenile floaters (Cam *et al.*, 1998). If floaters constitute a genetically-based alternative strategy (see above), their occupation of vacated territories may even

TABLE 5

Identification of questions and tasks for future research on the role of floaters in sexual selection.
 [Identificación de preguntas y tareas para investigación futura sobre el papel de los flotantes en la selección sexual.]

Question	Task
Is floating an alternative strategy?	Identify floater progeny and breeding floaters
What traits characterize floaters?	Identify and study floater phenotypes, manipulate traits involved in floaters status
What factors determine the occurrence and abundance of floaters?	Relate floater frequency to body size, longevity, mating system (monogamy-polygamy), social structure (cooperative, gregarious, solitary), breeding dispersion (colonial, dispersed), nest type (open, cavity)
Is floater status a transitory or permanent condition?	Follow floaters throughout their lifetimes
Is territorial behaviour in both sexes related to floater abundance?	Relate floater abundance to aggressiveness, frequency of take-overs, fighting injuries, lethal fights
Is sexual and social signaling in both sexes related to floater abundance?	Relate floater abundance to expression and intensity of signals involved in territorial defence and mate attraction
Is extra-pair behaviour in both sexes related to floater abundance?	Relate floater abundance to frequency of EPC and extra-pair progeny, male EPC tactics, female avoidance tactics
Is reproductive success of territorials affected by floater abundance?	Relate floater abundance to reproductive success in the population, study interference competition
Are estimates of the force and direction of sexual selection affected by consideration of floaters?	Compare selection differentials and gradients obtained including and excluding floaters

imply a reduced breeding performance as territorial breeders given their poor adaptation for this role. In general, colonisation by floaters of empty territories should not be considered an unmitigated plus for the conservation of endangered species. The buffer may to a high degree be made up by the poorer phenotypes in the population.

CONCLUSIONS AND FUTURE PROSPECTS

Several important issues require further research in order to clarify the role of floaters in sexual selection (table 5). Although floater individuals have recently been incorporated into the picture of population processes and conservation biology, their identity has seldom been established in field studies. Establishing the existence of “surplus” individuals depends on verifying the identity of non-territorial birds, a difficult proposition requiring specific programmes for marking individuals and so identifying each and every territorial bird in the study area. It should become a priority in avian studies to identify the floater fraction. Moreover, the implications of floaters in EPCs and egg dumping should be further clarified through detailed observational studies. Are most floaters really NR? It is insufficient to genotype nestlings; we need to genotype the floaters themselves. Another question raised is whether all floaters are involved in these alternative reproductive strategies. Genotyping is unable to detect the real NR fraction, for which observational studies of marked birds are necessary. The identification of floaters should be conducted across years to estimate the duration of exclusion status for individuals. How frequently do floaters change their status during their lifetimes? Is it a once-in-a-lifetime transition or can territorial status be lost after being acquired? Lethal or injurious exclusion should be quantified if possible to try to estimate the survival implications of floater

status. If a considerable fraction of natural populations suffers permanent exclusion from the breeding pool through competitive processes, the implications would be similar to those of the typical forces underlying natural selection, such as disease, predation, exposure and starvation.

Darwin (1871), the originator of the idea of competition for breeding resources and of sexual selection, wrote that selection processes unrelated to intraspecific competition –which he called natural selection– were probably stronger than those acting upon competition between individuals for participation in the breeding pool. In his view, natural selection was continuously removing a certain fraction of individuals from the breeding population by not allowing them to survive, while sexual selection just established the relative number of offspring of those able to breed. He was thereby underestimating the force that he was first to detect and understand. Sexual selection is also generating non-breeders, although they may be alive and healthy. In this way, by contributing not only to reduce but to prevent reproduction by a fraction of the population, it is shaping phenotypes for competition in both sexes. The levels of aggression and signalling exhibited by many birds may not be fully understood without considering that many individuals in natural populations never get a chance to breed. Existing phenotypes should express in their morphology, physiology and behaviour the relentless drive through evolutionary time to avoid this fate.

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