The great unknown – the floating stage as a neglected aspect of social systems

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Abstract

In the last few decades, important advances have been made in the knowledge on the behavioral ecology of pair-living primates such as owl monkeys (*Aotus* spp.). With the growing understanding, researchers have become increasingly aware that populations do not only consist of established family groups, but also of solitary "floaters": dispersing individuals who travel (mostly) solitarily after leaving their natal (or previous breeding) group and before obtaining a breeding position. Floaters may have a profound impact on local operational sex ratios and, thus, population dynamics, with the subsequent potential to change natural and sexual selection pressures on pair-living and sexually monogamous taxa. Unfortunately, floaters are notoriously difficult to study, so assessments of their role on social organization and mating systems remain challenging. Floaters of different taxa experience different selection pressures and employ varying strategies. In owl monkeys, a combination of limits to group size and habitat saturation forces all maturing individuals to become floaters as sub-adults or young adults, such that floating is essentially a life-stage in the species. The dispersal process is accompanied by increased tensions between adults and pre-dispersing individuals, probably due to various aspects of food and mate competition. Owl monkey floaters balance the need for prospecting with avoidance behavior towards groups, with whom they can engage in highly aggressive and potentially lethal interactions, by adapting their ranging behavior to spatial avoidance while seeking proximity at a temporal scale. Some fundamental aspects of floater biology on owl monkey societies (e.g. mortality rates, impact on population dynamics) are still poorly understood. We strongly suggest that floaters in all taxa where they occur are taken more consistently into

consideration and efforts are undertaken to improve understanding of their impact on group and population dynamics, and of sexual selection.

Background

It all seemed quite straight-forward. Owl monkeys live in pairs and mate monogamously (Huck et al., 2014, Fernandez-Duque, 2011). Once a year they produce offspring, who remain with the adult pair until they are three or four years old when they disperse (Fernandez-Duque, 2009). The dispersing sub-adults then enter a social group where they become reproducing residents. Since every breeding male is paired with one breeding female, there was to be little scope for intense competition, thus explaining the low sexual dimorphism. Only after several years of intense field work it became apparent that the picture was by no means complete, and that an important part of the social system of owl monkeys had not been considered. The behavioral ecology of the dispersing sub-adults had been left out of the considerations (Fernandez-Duque and Huntington, 2002). While it was assumed that they would find a new group and a partner, no research focused on what happened between their dispersal from the natal group and the joining of a new one. As so often before, research on birds has been a few steps ahead of that of primates and other mammals (e.g., Lack, 1968). It was research on owls (and other birds), not monkeys, that started bringing light to this aspect of the social organization and mating systems of owl monkeys (e.g., Campioni et al., 2010, Moreno, 2016, Penteriani et al., 2011, Rohner, 1997, Arcese, 1989).

An extensive body of mainly bird literature has looked at so-called floaters, individuals that are not living in established breeding pairs, despite being sexually mature, who move around within the population of breeders (Lenda et al., 2012, Newton, 1992). While in mammals there is a vast amount of literature on dispersal, the studies generally focus more on the aspect of group dynamics or sex differences in dispersal (Dobson, 1982, Greenwood, 1980), with usually less of a focus on the individuals' perspectives during the process of dispersal (but see for example Boyce and Boyce, 1988, Schradin et al., 2009). However, in some of these cases, the process is rather short; for example in the common vole (*Microtus arvalis*), dispersal does not last more than 24 hours, so there is not a pronounced floating period (Boyce and Boyce, 1988). As terms such as floater or dispersal are often not consistently used, we thought it prudent to provide our usage of some definitions for basic terms (Table 1).

Table 1 approximately here

In the following, we first summarize various research questions about floaters, organizing them into discrete hypotheses, and derived predictions (sub-header numberings correspond to numberings in Table 2). At the end of each section, we then focus on the available evidence for these hypotheses for Azara's owl monkeys (*Aotus azarae azarae*) and highlight where further research is needed. Throughout the chapter we refer to this species as owl monkeys; readers should be aware that similar evidence is not available for any of the other *Aotus* species (García de la Chica et al., this volume).

Since it is beyond the scope of a review chapter to provide the full details of the methodology used in published research from the Owl Monkey Project, we offer here a brief summary. Behavioral and demographic data collection began in 1997; since 2000 demographic data have been collected from 27 groups. For main study groups at least one adult group member was radio-collared to facilitate location of groups and identification of individuals (Fernandez-Duque and Rotundo, 2003, Juárez et al., 2011). For 18 groups, several years of observations with at least one marked individual resulted in 238 group-years, as well as information on 43 floaters. For 22 of these we also have some focal observations (for details of demographic and behavioral data collection see e.g., Huck and Fernandez-Duque, 2012).

As we consider the process of dispersal in more depth elsewhere (Corley and Fernandez-Duque, this volume), one of the most fundamental considerations of floating as a stage is whether it is an Alternative Reproductive Tactic (ART), simply a life stage without reproduction, or an indication of inferior genetic quality. After discussing ARTs we then turn to the question of why dispersing individuals do not simply settle down immediately and form a new group and what influences the duration of the floating stage. We follow with "day-to-day" considerations of the lives of floaters, and finally the impact they could have on population dynamics and intra-specific selective forces.

I. Is floating a life-stage that all individuals undergo, an indication of inferior genes, a conditional tactic, or an equal-fitness alternative reproductive tactic?

Exploring this question (Table 1 for definitions, Table 2 for an overview of related hypotheses and predictions) leads us to examine how it is "decided" who breeds, and who floats. The mechanism may be simply an age effect ('Life stage hypothesis'), where all individuals reaching a certain age class leave their natal group and later, if they survive the floating stage, become territorial. If floating is a life stage it cannot be considered an Alternative Reproductive Tactic (ART), because there is no alternative. However, there may still be variation *within* the floater cohort, for example how far they disperse or for how long individuals float. In red squirrels (*Sciurus vulgaris*), for example, all young disperse, but some disperse long distances, undergoing presumably a longer floating stage, while others settle directly in neighboring territories, where both tactics have the same fitness (Wauters et al., 1994).

Contrary is the hypothesis that floaters are genetically inferior individuals ('inferior genes hypothesis'; e.g., Lenda et al., 2012). This hypothesis states that not all individuals become floaters, but that fitter individuals will be able to breed as soon as they mature sexually and, in contrast to any of the other hypotheses, leads explicitly to the prediction that if floaters obtain a reproductive position, reproductive success would be lower than for individuals that did not become floaters (Lenda et al., 2012). In song sparrows (*Melospiza melodia*), for example, some yearlings acquire a territory and mate, and some become floaters. Song sparrows that obtained a territory and mated already as yearlings had a higher life-time reproductive success than floaters, although the overall sample size was too low to draw very strong conclusions (Smith and Arcese, 1989). Fitness of the offspring of former floaters and direct breeders were not compared in that study. The 'inferior genes' hypothesis implies a conditional strategy, suggesting a genetic polymorphism. However, conditional strategies do not require a genetic underpinning of "status", because age effects or differences in habitat quality could lead to temporary, reversible changes in body condition, health, parasite load, or similar indicators of status (Table 1, Glossary). Indeed, in the original framework of Gross (1996), a conditional strategy is explicitly genetically monomorphic. We therefore contrast the 'inferior genes' hypothesis with a broader sense 'conditional strategy' hypothesis that does not imply that status is irreversible. In this scenario, floaters could choose to delay territorial breeding when the reproductive costs are higher for inexperienced individuals, meanwhile making 'the best of a bad job' by sneaking copulations (Yasukawa, 2013). While the social structure of Sumatran orang-utans (*Pongo abeli*) is perhaps not completely comparable to a typical floater system, they show a pronounced bi-maturism of males. Large, flanged males consort with females and small, unflanged ones try to sneak copulations from sometimes unwilling females, which could represent a conditional strategy (Utami et al., 2002). Floaters could also wait (or 'queue') to obtain higher quality territories in the future (Zack and Stutchbury, 1992). In African striped mice (*Rhabdomys pumilio*) individuals can employ three alternative reproductive tactics (ARTs, Table 1): group living territorial breeders, group living philopatric males, and solitary floaters or 'roamers' (Schradin and Lindholm, 2011). Which tactic they employ depends on population density and body mass (Schradin and Lindholm, 2011). Under high population density, the situation appears to be a conditional strategy with highest success for territorial males, but at intermediate densities, success of floaters and territorial males have similar success, suggesting rather a mixed strategy (Schradin and Lindholm, 2011), or in our framework, an 'equal-fitness alternative reproductive tactic' (efART; Table 2), which is a combination of what Gross (1996) called Alternative Strategies and Mixed Strategies (see Table 1 for further explanations). Both are frequency dependent evolutionarily stable strategies. Under the efART hypothesis extra-pair copulations could result in equally high or, frequency dependent, even higher fitness for floaters than breeding in pairs. The latter possibility has been tentatively suggested for tree swallows (*Tachycineta bicolor*), where about half of all offspring are not sired by the male of the pair; of the 65% of extra-pair offspring for whom the father was determined, 20% were sired by floaters (Kempenaers et al., 2001). This could be a substantial under-estimate if the un-identified extra-pair fathers were more likely to be floaters than resident breeders, given that floaters are more difficult to catch than residents (Kempenaers et al., 2001).

These hypotheses have partly overlapping predictions. Under the ‘Life stage hypothesis’ we assume that all individuals of the dispersing sex, or sexes, will become floaters. Contrary to this, under the other three hypotheses, one predicts that not all dispersing individuals that *can* become floaters will do so, as evidenced by frequent intrusion attempts by spotless starlings (*Sturnus unicolor*; Veiga et al., 2012). Under the 'inferior genes' and 'conditional strategy' hypotheses no voluntary switches from breeder to floater would be expected. Thus, in African striped mice philopatric males can switch to floaters or territorial males and floaters can switch to territorial males, but switches the other way round were never observed (Schradin et al., 2009). Switches from territorial breeders to floaters would be expected if floating is an equal-fitness ART. For example, in tree swallows, while the evidence so far remains anecdotal, there was a case of a resident male who became a floater without being challenged by an intruder, and vacancies were filled by other residents, rather than by floaters, even though these were available (Kempenaers et al., 2001).

The three hypotheses also lead to different predictions with respect to body condition (Table 2). If floaters are of innate inferior quality compared to individuals living in groups, as implicitly assumed by Lenda et al. (2012), some aspects of their physical condition, such as body mass or parasite load, should be consistently poorer in floaters and, importantly, would also remain poorer after a floater obtains a breeding position. We did not find a study providing supporting evidence for this. In contrast, if floating is a life stage or a conditional tactic, then floaters may temporarily have lower body condition during the period of floating. Floaters may be less efficient while foraging, for example because the requirement for vigilance behavior is higher in solitary individuals (e.g., in willow tits, *Poecile montanus*; Hogstad, 2014) or due to harassment by groups (e.g., spotless starlings, *Sturnus unicolor*; Veiga et al., 2012). However, once they become breeders, they will recover their condition, as clearly shown in African striped mice (Schradin et al., 2009). If floating is an equal-frequency alternative reproductive tactic, floaters can have even higher body condition than breeders. In tree swallows, floaters were actually heavier than residents, and males that sired extra-pair young (floaters and other residents) had less bite holes by mites in their feathers than resident males without extra-pair young (Kempenaers et al., 2001). While the equal-fitness ART hypothesis requires that the mean fitness of floaters be similar to that of resident breeders, under the other hypotheses, floaters have lower fitness than resident breeders, but individuals may still attempt to ‘make the best out of a bad job’ and try to obtain extra-pair copulations during the floater stage. Thus, in New Zealand hihis or stitchbirds (*Notiomystis cincta*), floaters commonly reproduce even though their reproductive success is lower than that of territorial males (Brekke et al., 2015).

For owl monkeys, all evidence points towards floating being a life-stage. Most individuals who survive the floater stage become breeders in fixed territories (Fernandez-Duque, 2009, Huck et al., 2011), with 46 immigrations (in 238 group years on 18 groups) resulting in pairs with breeding success, while only 9 immigrants disappeared or died before reproduction. This is rather an overestimation of unsuccessful immigrations because the existing pairs with offspring at the start of observations were not counted as successful immigrations, even though we have no evidence that there was ever a case of an offspring inheriting the natal territory. Therefore, floaters are not generally genetically inferior to home range holders, since all territory holders had been floaters before. The 'inferior genes hypothesis', therefore, is not supported. Whether unsuccessful floaters, however, are inherently different to successful ones cannot be determined because we do not know enough about the fate of floaters in general, and those disappearing out of our study area in particular. Floating does not seem to be a conditional or an equal-fitness Alternative Reproductive Tactic, given that owl monkey floaters do not reproduce (Fernandez-Duque and Huck, 2013). We have never observed a solitary individual with offspring born outside a pair, and have no evidence that floaters copulated with resident breeders based on 21,734 h of contact time with groups, of which 767 h (incl. 35 hours of focal observations) were conducted on floaters (Owl Monkey Database up to 28 June 2020). In contrast, in 2,470 h of focal time on groups we observed 85 copulations. Furthermore, genetic analyses showed for 35 infants (from 17 different pairs) that all were sired by the male who was resident at the time of conception (Huck et al., 2014). Additionally, no primary floating female has ever been observed with an infant.

TABLE 2 APPROXIMATELY HERE – EXACT PLACEMENT DOES NOT MATTER TOO MUCH

II. Why do dispersing individuals become floaters instead of forming new groups/pairs?

If floaters can only make the best-of-a-bad-job, or even entirely fail to breed, the question arises why they should float. Most likely this is a consequence of competition for territories or mates (Smith and Arcese, 1989, Penteriani et al., 2011). The 'habitat saturation hypothesis' assumes that the population is at its carrying capacity, with no available breeding territories that floaters can occupy. The not mutually exclusive 'limited sex hypothesis' states that due to an uneven adult sex ratio (ASR), or operational sex ratio (OSR, see Table 1 for definitions), one sex is in surplus and individuals of that sex cannot find reproducing partners. In birds, it is usually males that are in surplus (Donald, 2007, Moreno, 2016), while at least in ungulates adult sex ratios are more commonly shifted towards females (Berger and Gompper, 1999). Due to the higher polygamy potential, however, the OSR is commonly assumed to be male biased in most mammals (Emlen and Oring, 1977). In polygynous mammals, males are commonly the dispersing sex. Sometimes, for example in geladas (*Theropithecus gelada*), South American squirrel monkeys (*Saimiri sciureus*) or African lions (*Panthera leo*), dispersing individuals form bachelor groups (Snyder-Mackler et al., 2012, Funston et al., 2003, Mitchell, 1994). Many birds, however, are pair-living, and in many species the ASR is male biased due to higher female mortality (Donald, 2007). This necessarily means that some individuals will not find a partner within a pair.

In owl monkeys, habitat saturation, but not limited partner availability, explains why floaters do not form their own groups. In Argentina, both at the Owl Monkey Project main field site in the Estancia Guaycolec (58°11’W, 25°58’S, Fig. 2) and in the Parque Nacional Río Pilcomayo 200 km away (25º56’S, 58º13’E), the entire habitat that is suitable for owl monkeys is densely packed with groups (Juárez, 2012, Huck and Fernandez-Duque, 2017, Wartmann et al., 2014). In the humid Chaco of Argentina and Paraguay, suitable habitat consists of continuous gallery forests along rivers and naturally occurring patches of forest. The median size of inhabited forest patches is 7.7 ha (mean range = 13.0 ha; recalculated from Juárez, 2012). Groups have overlapping home ranges that are fairly stable, and there is no unoccupied suitable habitat (Huck and Fernandez-Duque, 2017, Wartmann et al., 2014). The savannah matrix between patches of forest islands and bordering gallery forests is not suitable permanent habitat, even though individuals occasionally cross it to reach other locations during dispersal (Corley and Fernandez-Duque, this volume). Neighboring home ranges sometimes differ widely in fruit availability, although there is some evidence that certain fall-back foods are more evenly distributed during the dry season when considering the core areas of the home ranges (van der Heide et al., 2012). Given that both sexes disperse (Corley and Fernandez-Duque, this volume) and individuals of both sexes “float” (Fernandez-Duque, 2009, Huck and Fernandez-Duque, 2017), there are potentially available partners moving solitarily. Still, although pairs of floaters are seen sporadically together for a few hours or days (34 out of 1352 encounters with solitaries = 2.5%), these associations never last long and we have only a single instance where we saw the same floater on three consecutive days with a partner (Owl Monkey Database (OMD), unpubl. data).

III. What determines the duration of floating or proportion of floaters?

The hypotheses discussed above raise the question of whether a sub-adult or young adult should float or not, and also suggest likely variability in the duration of the floating stage or the proportion of floaters within a given year. And like the previous hypotheses, duration of floating or relative proportion of floaters could well depend on the frequency of other individuals– be it breeders or other floaters of the same sex. Duration of floating, and thus indirectly proportion of floaters, can then be viewed as conditional or equal-fitness alternative tactics, even if floating itself is a non-reproductive life stage. It can be hypothesized that the duration of floating depends at least partly on the number of available breeding positions, territories or other relevant essential resources relative to the number of floaters in an area. This frequency-dependency can also be expected if floating is a life stage (I.1). Alternatively, but not entirely mutually exclusive, floating duration could be related to individual quality. This does not assume a generally lower quality of floaters *per se*, but only, that individual floaters can differ in quality, whether genetically or due to better conditions while they grew up, and that these differences can influence the duration of floating. For birds it has been noted in a recent review (Moreno, 2016), that few studies have been able to determine the duration of the floating stage, and indeed we found no studies that would directly support these suggestions. Indirect evidence for frequency dependency (and partly an impact of quality) comes from spotted starlings (*Sturnus cineraceus*), where the provision of additional nest boxes after the first round of breeding had already started, enabled previously floating individuals to occupy these nest boxes and successfully breed (Saitou, 2001). The same study also suggested, but did not provide direct evidence for this, that floaters had been outcompeted initially, indicating inferior quality, and tried to compensate by alternative tactics such as brood parasitism (Saitou, 2001).

Additionally, or alternatively, the proportion of floaters in a population could also be influenced by the quality of the habitat ('habitat quality hypothesis'). When discussing the ‘habitat saturation hypothesis’ above, habitat was viewed as of an essentially homogenous quality. However, potentially suitable habitats are likely to vary, with lower quality habitat leading to lower reproductive success (Chaney et al., in preparation, Wood and Fernandez-Duque, in preparation). For example, in savannah baboons (*Papio cyanocephalus*, *P. anubis*, and their hybrids), inter-birth intervals were shorter in higher quality habitats than in poor ones (Gesquiere et al., 2018). Thus, individuals in populations where all high-quality territories are occupied, but some lower quality areas are still available, may face the choice of whether to settle down in a low-quality patch or to float. Assuming the same number of territories and population density, one predicts then that in areas where the differences in habitat quality between high (occupied by established long-term breeders) and low-quality territories (occupied by young first breeders) is smaller than usual, the number of floaters will be lower and the number of young first-time breeders higher. On the other hand, in poor-quality areas the relative frequency of floaters will be relatively higher and the number of young first-time breeders lower than usual. This does not mean that the number of first-time breeders is higher in absolute numbers than that of floaters, or vice versa. Similar predictions can be formulated for the temporal dimension, comparing "good" and "bad" years.

While all owl monkeys who survive the juvenile stage become floaters, **the duration of this stage is rather flexible**. We have no data to evaluate whether the duration could be dependent on the condition of the floater. For nine primary floaters (6 males, 3 females) of known floating duration, the stage lasted between 5 days and 15 months (mean: 5.8 mo., median: 3.8 mo.), with no obvious difference between the sexes (range males: 0.7 - 13.2 mo, mean 5.2 mo; range females: 5 days – 15.2 mo, mean 5.2 mo). Yet, when considering individuals whose data are right or left censored (i.e., no date for becoming a breeder, or no date for leaving their natal group), the mean was substantially longer with a mean of 8.8 and a median of 4.8 months (N=27; OMD, unpubl. data). We do not know, currently, what determines the duration of the floating stage. It could depend on the number of other floaters in the area relative to the potentially available breeding positions, the condition of the floater, or both. The potentially available breeding position in turn is likely to depend on mortality risk of breeders or their health status. Information on body condition when dispersing and later entering groups and the number of individuals floating in the area at the same time is therefore required, but currently incomplete or unavailable.

IV. What is a floater’s tactic to become a resident?

Whether they float for a long or short period, floaters are likely to attempt to become resident breeders (unless it is an equal-fitness alternative reproductive tactic). The tactics they can use are either to ‘sit-and-wait’ or to ‘prospect’. Using a sit-and-wait tactic, a floater will, after an initial phase of moving away from the previous group, settle in a relatively clearly defined range, as observed in eagle owls (*Bubo bubo*; Penteriani and Delgado, 2012). The initial dispersal phase may be very short, if it settles close-by, or last longer if it moves further away. The floater will then remain in this area and wait until an opportunity arises to move into a vacant territory (Rohner, 1997), or even forcefully create such a vacancy by evicting a resident neighbor like in song sparrows (Arcese, 1989). Floaters also may continue moving, or make regular forays, to investigate whether a vacancy has arisen, or if any residents are weakened and easier targets for eviction. The importance of familiarity with sites for successful territory acquisition by floaters has been shown for oystercatchers (*Haematopus ostralegus*; Bruinzeel and van de Pol, 2004). While these two tactics may be considered mutually exclusive, an individual floater conceivably could switch from one to the other, or within a species, some floaters could employ one tactic, and others another.

In owl monkeys, individual floaters may combine a sit-and-wait with a prospecting tactic, where floaters **try to balance the need for obtaining information on groups with the risk of getting attacked by residents**. This conclusion is based on the findings that floaters seem to stay close to resident groups at any given time (i.e., comparing time-matched locations of floaters and groups) while still avoiding the groups' core areas and mainly using the borders of the ranges of groups (Huck and Fernandez-Duque, 2017).

V. Are there differences between (types of) floaters?

As explained above (section IV), some floaters may remain relatively close to their natal territory, while others, or at a different stage of dispersal, may move far away from it (Delgado and Penteriani, 2008, Solmsen et al., 2011, Wauters et al., 1994). Furthermore, depending on the dispersal pattern of a species, either only one sex may include floaters, or both, and there may be sex differences in the duration of the floating stage. Theoretically, in pair-living species with life spans that cover several breeding seasons, one expects both sexes to disperse, and this should lead to floaters of both sexes if territories (or nesting sites or other crucial resources) are rare, and if there is an equal sex ratio. However, in many bird species, floaters seem to be predominantly male (reviewed in Moreno, 2016), which is in line with the commonly male-biased adult sex ratio in birds (see II). There may also be floaters of different age groups, and this could link to different reasons why individuals become floaters. For example, natally dispersing individuals may be the primary source of floaters (I.1), but older individuals that have obtained a breeding position may become secondary floaters by either forceful evictions (e.g., song sparrows: Arcese, 1989, Olympic marmots, *Marmota olympus*: Arnold, 1990) or by voluntarily dispersing due to incompatibility with the mate (Dubois and Cézilly, 2002). In these latter cases, though, it seems more typical that they switch to a different partner rather than floating (e.g., in oystercatchers; Ens et al., 1993). Due to their different reproductive success expectancies, secondary floaters may adopt riskier strategies than primary floaters (see Table 1 for definition). That older individuals with a lower remaining reproductive value can indeed employ riskier or bolder tactics has been shown experimentally in as diverse species as Australian field crickets (*Teleogryllus oceanicus*) and grey mouse lemurs, *Microcebus murinus* (Dammhahn, 2012, Moschilla et al., 2018).

Even though we expect relatively few differences between male and female owl monkey floaters (see III & VI), floaters are unlikely to be a homogenous category. While there is some tentative evidence for differences between primary and secondary floaters (for details see section IX), we know very little about the behavior of secondary floaters. The few we have followed have mostly perished relatively quickly. Therefore, the following considerations refer to primary floaters. To find groups that have either a breeding vacancy or where the same-sex resident can be challenged, floaters can stay close to a limited number of groups, using a sit-and-wait approach, or they can roam over a far larger area for prospecting (‘transient floaters’, see VII for more details). Unfortunately, an evaluation of those two tactics is constrained by methodological issues. Consistent data collection on floaters can only take place if they are radio-collared and can be recognized and followed individually despite their cryptic behavior (Fernandez-Duque et al., this volume). The range of the VHF transmitters we have used is about 1000 m; thus, individuals that leave the study area are frequently outside the range of our receivers during routine field work. Unless we survey regularly outside the core area of study, we are more likely to obtain regular data from ‘waiters’.

VI. When and how do individuals become floaters

Additional to the ultimate considerations above, we also need to understand the proximate factors that influence dispersal (Fig. 1). To understand the importance of floaters for population dynamics and selective pressures acting on individuals it is necessary to know the ecological, environmental, and social factors that may influence when individuals join the pool of floaters. The various factors are not mutually exclusive and can have combined effects on dispersal, though some may be more strongly linked than others. For example, under the ‘Life stage hypothesis’ it is predicted that floaters will be of a specific age group, while under the ‘Inferior genes hypothesis’ or the 'equal fitness ART hypothesis', a less defined age range is expected. Rather than age, it may be that it is a critical body mass, or condition, that individuals need to reach before they leave the natal group. Thus, male, but not female, banner-tailed kangaroo rats (*Dipodomys spectabilis*) under experimentally supplemented conditions were heavier and dispersed earlier than the un-supplemented control group (Edelman, 2011), and there was a similar difference between provisioned and un-provisioned Belding’s ground squirrels (*Spermophilus beldingi*) (Nunes et al., 1999). However, having a higher body mass than other peers of similar age does not necessarily trigger dispersal; Olympic marmots dispersers had a similar body mass than same-age non-dispersers, and had actually lost more weight in the previous winter than non-dispersers (Arnold, 1990).

Fig. 1 approximately here

In many species, dispersal happens around sexual maturation, which will usually occur at a specific age (Wada, 2008). It could be expected that pre-dispersing individuals will show sex hormone levels that are approaching adult levels, and that floaters already have, or are reaching adult sex hormone levels. In common voles (*Microtus arvalis*), sexual maturity is reached shortly before dispersal (Boyce and Boyce, 1988). Female chimpanzees (*Pan troglodytes*) have their first maximal swelling at around 10.7 years old and emigrate at a mean age of 11.3 years (Nishida et al., 2003); and in Mongolian gerbils (*Meriones unguiculatus*), males expelled from the group had larger testes than those allowed to remain (Scheibler et al., 2006). Even when there is an increase in testes size in juvenile male savannah baboons as adolescents they still undergo a period of reproductive quiescence which coincides with the time they usually disperse (Onyango et al., 2013). In some species, however, dispersal occurs in juveniles who have not yet reached adult sex hormone levels, for instance in female muriqui monkeys (*Brachyteles arachnoides*; Strier and Ziegler, 2000) or male Belding’s ground squirrels (Nunes et al., 1999). In other species, sex hormones can be even higher in floaters than in territorial breeders, such as in striped mice (Schradin et al.,

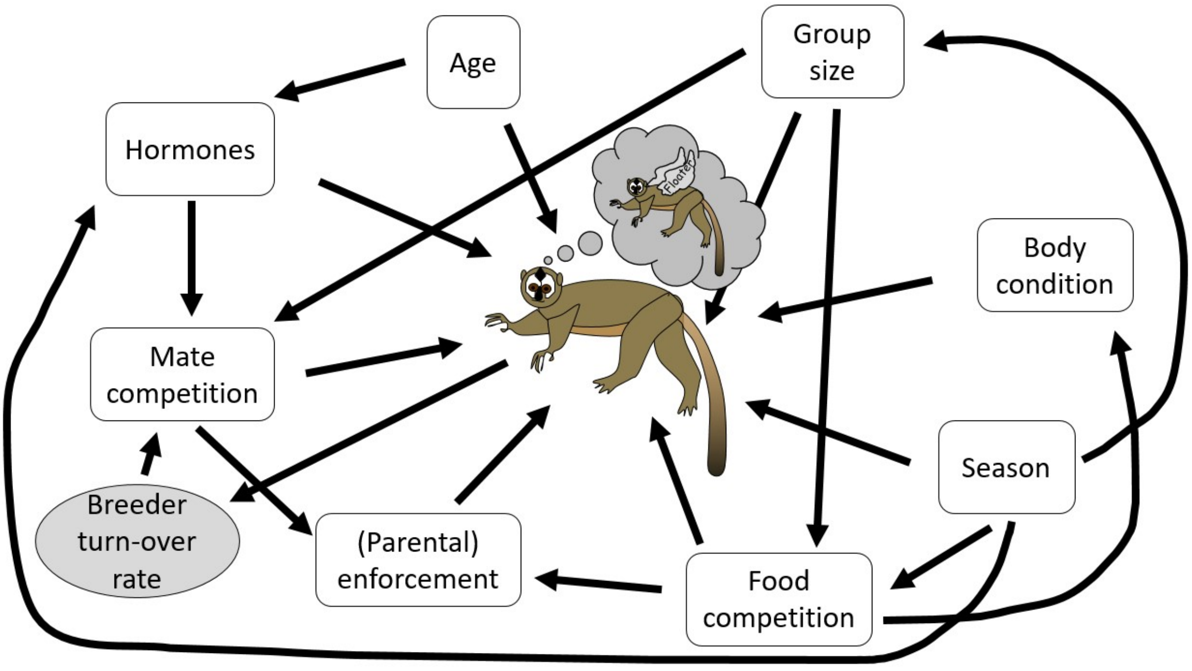

Fig. 1: Proximate factors that may affect when and how individuals become floaters. Note that these relationships are not owl monkey-specific and that additional interactions are possible.

2009). Glucocorticoids are also commonly associated with dispersal (Wada, 2008). In striped mice the probability of disappearing increases for light individuals with higher cortisol levels, and it was suggested that this could be an indication that the hormone triggers dispersal (Vuarin et al., 2019).

In longer-lived species, particularly in mammals but also some co-operative birds, juveniles may stay for several years within their natal group. The influence of age can then be further modulated by, for example, season, group size, or competition for food or mates. If the reproductive season is relatively long, individuals of slightly different ages will still disperse at the same time, if conditions for dispersal are optimal in certain seasons, or, contrarily, if competition for food becomes most severe at specific times. Especially when juveniles from several reproductive events are present in groups, group size can be a factor favoring dispersal (Arnold, 1990). Age, group size, hormones, or seasonality can prompt emigration directly, or through the interactions of pre-dispersing individuals with adults in the group (e.g., western slaty-antshrike, *Thamnophilus atrinucha*; Tarwater and Brawn, 2010). As a shorthand, we refer to this as ‘parental enforcement’ (Table 1), even when adults in the group are not necessarily biological parents. In groups where adults are not always related to the (pre-)dispersers, mate competition can also promote dispersal, with or without aggression (Mongolian gerbils: Scheibler et al., 2006, e.g., Siberian jay, *Perisoreus infaustus*: Ekman and Griesser, 2002).

Finally, local or inter-annual variation in food competition could affect the parents’ tolerance of offspring. It can be predicted that parent-offspring conflict increases in harsh years, leading to earlier dispersal; it is also likely that the effects of harsh years are conditional on group size. Effects of habitat quality can affect sex ratios that can be linked to the dispersing sex, as proposed for Arctic foxes (*Alopex lagopus*), where more males reach maturity on poorer patches than high quality patches, presumably because males are the predominant dispersers (Goltsman et al., 2005). If territories only support groups of a maximum size even in optimal years, then older offspring will disperse at the latest when this maximum size is reached. What the maximum group size is, will be related to local or yearly variations in habitat quality.

Owl monkeys disperse mostly during a specific age-range, i.e., sub-adulthood, as it is the case for other species where primary floating is a life-stage rather than a tactic. Males and females disperse between 2.3 and 5 years of age, with a mean and median of 3.7 (± 0.7 StDev) years for both sexes(values are slightly updated using the latest OMD data from Huck et al., 2011, Fernandez-Duque, 2009). However, it is unclear what are the internal and external factors that lead some individuals to disperse as young as 2.3 years of age, and others after turning five years old (with the oldest dispersal age recorded at 5.3 years of age). Reaching a critical body mass and different trajectories of sexual maturation ought to be examined, but the number of individuals is still relatively small for identifying robust patterns. Nevertheless, hormonal data of 11 juvenile and sub-adult females, indicated that female owl monkeys start cycling before they leave the group, albeit more irregularly than fully mature ones (Corley et al., 2017a, Corley and Fernandez-Duque, this volume, Corley et al., this volume). Whether a similar endocrinological pattern occurs in males, and whether differences in speed of maturation relate to the time-lag to dispersal, still require investigation.

The age and maturation status, as primary likely factor regulating the dispersal phase in owl monkeys, is probably moderated by aspects of intra-group competition for resources. It is likely that there is a maximum group size (Fernandez-Duque et al., 2001) given that groups have never had more than seven members including infants. These groups of seven, which occur rarely and only during the birth season, usually lose a few months later a dispersing animal. Nevertheless, dispersal is possibly rather related to a group-specific maximum group size than a simple measure of groups size; yet a larger sample of dispersal events with known ages from well-monitored groups are needed (Fernandez-Duque and Huntington, 2002). Furthermore, while it can occur throughout the year, in our population **dispersal occurs most frequently during the Spring, which is also the birth season** (Fernandez-Duque, 2009, Fernandez-Duque and Huntington, 2002). At this point, we cannot adequately characterize the interplay between sub-adult owl monkeys leaving “on their own free will” or following enforcement by the adults. **There is, at least in some cases, a component of enforcement**. Agonism from the adults in the group towards subadults increases shortly before a sub-adult leaves the group (Corley et al., 2017b; see also example of ‘Enrique’ below). In owl monkeys, intra-group competition could be related to both food competition and mate competition, if the opposite-sex parent had previously been replaced by an unrelated intruder, i.e., a 'step-parent' (Fernandez-Duque and Huck, 2013).

Food limitation is likely a primary source of competition in owl monkeys that may be modulating dispersal. Measuring resource availability in (sub-)tropical climates is difficult, in particular if the species utilizes a large variety of food sources like owl monkeys (van der Heide et al., this volume, van der Heide et al., 2012). However, currently we do not have sufficient data on fruit availability and dispersal instances to explore possible causal relationships between food and dispersal. Some suggestive evidence comes from the difference between owl monkey groups living in continuous gallery forests and those living in forest islands that are situated in a matrix of savannah habitat (Juárez, 2012). Group sizes and birthrates on islands are consistently smaller than for groups in gallery forests, even if islands can be larger than the average range size of groups in gallery forests (Juárez, 2012, Fernandez-Duque et al., 2001). While plant diversity (e.g., richness and Shannon diversity) is not necessarily different between islands and gallery forest (Briggs et al., 2019), we do not have a clear understanding of the availability of owl monkey food plants on islands with and without monkeys. That being said, a preliminary 2-month study found that fruit availability was higher in the gallery forest than in forest islands, and that this difference was also related, in summer, to those fruits consumed by owl monkeys (Giménez, 2004). This was also reflected in some behavioral and dietary differences between the two groups compared, with longer foraging times and a broader diet in the forest island (dry forest) group. It is therefore conceivable that because groups in forest islands cannot as easily exploit areas beyond their normal home-range in times of extreme scarcity as groups in continuous forest, their maximum group sizes are more limited than for gallery forest groups.

Mate competition can also, even if only occasionally, occur in some family groups. As a pair-living, sexually monogamous species (Huck et al., 2014), the group is quite frequently formed by biological parents and their offspring. When considering only pairs that stayed together to reproduce at least one offspring, the median pair-duration for 26 pairs was 9 years (Fernandez-Duque and Huck, 2013). Thus, we do not expect competition of offspring with their same-sex parent over the opposite-sex parent (Huck et al., 2014). However, turn-over of breeders is common, with 27 female and 23 male replacements in 149 group years (Fernandez-Duque and Huck, 2013). This leads to the frequent presence of step-parents and step-siblings in groups, where 32 out of 58 infants (55%) experienced the replacement of at least one parent (Huck and Fernandez-Duque, 2012). While step-parents behave to young step-infants just as they would to biological offspring, there is an increased tension between same-sex step-parents and maturing sub-adults (Huck and Fernandez-Duque, 2012, Corley et al., 2017b). A case in point is 'Enrique', who dispersed at the relatively old age of 51.5 months just after his mother disappeared (Huck and Fernandez-Duque, 2012). He rejoined his natal group three months later; by then a step-mother had replaced his mother, while his biological father 'Fabian' was still present. After trying to copulate with his step mother, Enrique was aggressively chased away by Fabian, who even bit him and chased him to the ground, so that he again left the group (Huck and Fernandez-Duque, 2012, García de la Chica et al., 2020). Furthermore, close proximity between an immature and an adult, a proxy for an affiliative relationship, decreased between pre-dispersing offspring and their same-sex parent after the intrusion of an opposite-sex step-parent (Huck and Fernandez-Duque, 2012). Interestingly, there was no decrease in dispersal age after an opposite-sex adult was replaced, but the time-lag between the arrival of a step-mother and dispersal of young females was shorter than after the arrival of a step-father. This finding would indicate that the offspring is delaying dispersal when potential mating opportunities arise within the group (Huck and Fernandez-Duque, 2012). However, we do not yet have any evidence that a natal sub-adult replaced their own parent when a step-parent of the opposite sex entered the group. Currently, sample sizes are too small, with many confounding variables, to obtain a clear picture on whether mate competition regularly forces sub-adults to become floaters.

VII. What does best explain the ranging pattern of floaters?

It is very likely that floaters differ behaviorally from individuals living in established groups. This is, indeed, implicit in the very term 'floater', which implicates that ranging patterns differ between floaters and established groups. How exactly these patterns differ is likely related to the tactic floaters employ to become residents (section IV). If floaters employ a sit-and-wait tactic they will have lower food requirements than those of a group of several individuals; thus, their range should be smaller, unless they range in marginal habitat. Differing demands could be behind the pattern found in Eagle owls, where floater ranges are 44% smaller than those of breeders, but core ranges are 36% larger, and nightly movement rates within core areas are 17 times higher (Penteriani et al., 2015). Temporal activity phases likewise can differ between floaters and breeders, as again evidenced in Eagle owls (Penteriani et al., 2015). Yet, if floaters employ some form of prospecting, they will range over many group territories, leading to either particularly large ranges (mixing sit-and-wait with prospecting), or a shifting range (if prospecting is continuous). For example, in African striped mice non-territorial male 'roamers' have larger home-ranges than philopatric and territorial breeding ones (Schradin et al., 2009).

The ranges used by owl monkey floaters (measured as 95% kernels) varied between 5.2 and 201 ha (mean: 39 ha, median: 24 ha, 24 floaters Huck and Fernandez-Duque, 2017, these values are not provided in the article, but based on the original data). The ranges of male (mean = 36.8 ha, median = 34.8 ha, N = 8) and female floaters (mean = 41.3 ha, median = 20.2 ha, N = 16) are similar (Welch t-test, t = 0.3, df = 19.7, p = 0.74). Even for ‘waiters’, **floaters’ ranging patterns thus differ from those of established groups**, as group ranges had a mean size of 6.1 ha (median 5.7 ha, range 3.5 – 9.5 ha, N=15; Huck and Fernandez-Duque, 2017). For most floaters we do not have sufficient data to calculate separate home ranges for different time-periods, but the cases of females 'Emma' and 'Sepia' indicate that **individuals seem indeed to follow different tactics**, with some staying close to their natal range, and others moving more considerable distances**.** Emma had the smallest range (5 ha, 23 radio locations, spanning 22 months), whereas Sepia had the largest (201 ha: 75 radio locations, spanning 17 months of tracking). A task for the future could be to compare floater behavior, for example whether they stay close to the natal range or move further away, depending on whether or not the presence of an opposite-sex step-parent would offer the opportunity to become a breeder in the natal territory.

VIII. Do activity patterns of floaters differ from those of groups?

The decision whether or not to live in a group or solitarily is based on the relative costs and benefits of either option (Pulliam and Caraco, 1984). For species that usually are considered group living, it is likely that floaters face some of the disadvantageous elements of a solitary lifestyle that are normally avoided by group living. Depending on the individual characteristics (e.g., age, body condition, sex), the structuring of a 24-hr activity pattern will require stronger attention to predator avoidance, prospecting, or the avoidance of established groups, while predictions about feeding patterns are less straight-forward. In species where predation is a high-risk factor, floaters will be more vigilant and spend relatively less time sleeping than a member of an established group. In willow tits, winter-floaters scanned their surroundings more and foraged less than territorial flock members

(Hogstad, 2014). In African striped mice, daily mass-specific energy expenditure and resting metabolic rate was higher in floaters than in territorial males (Rimbach et al., 2019). On the other hand, energy requirements could theoretically be reduced if there is no need for territory or mate defense, or if food competition is high within groups. Floaters are also expected to behave as inconspicuously as possible, possibly vocalizing less and moving in a more careful manner. This will enforce the difficulties of detecting floaters if, in contrast to residents, they do not respond to playback calls, as in long-horned owls (*Bubo virginianus*) or willow tits (Hogstad, 2014, Rohner, 1996), or select more hidden perching posts, as in eagle owls (Campioni et al., 2010).

Floaters are furthermore likely to face aggression from established groups. Circumstantial evidence suggested that cheetah (*Acinonyx jubatus*) floaters were killed when they challenged territory holders (Melzheimer et al., 2018). If encounters with residents have serious consequences, floaters are expected to remain as 'invisible' as possible, behave cryptically, and to possibly shift activity patterns to different times of the day, or avoid core areas of group territories. There will be necessarily some kind of trade-off between avoiding groups and the need for prospecting (see section IV). The extent of behavioral shifts away from typical group patterns can thus provide some indication on selective pressures for floaters, as well as for breeders.

Apart from the differences in ranging patterns, **we do not know much about the behavior and activity patterns of owl monkey floaters**. The predictions around their activity patterns need to be tested with the available data from our 25-year data base. This can, however, prove problematic since the 'predator avoidance hypothesis' leads, additionally to the predictions stated in Table 2, to the prediction that solitary floaters should react more strongly to the presence of human observers, which could bias data collection on them much more strongly than that of our well-habituated groups.

IX. The perspective of resident breeders

It is important to consider the perspective of resident breeders when studying the behavior of floaters, too. The 'dear-enemy hypothesis' states that groups will reach a state of truce with familiar neighboring groups (Fisher 1954, cited in Christensen and Radford, 2018). As the adults in groups of pair-living species will have established breeding positions, the risk of forceful take-overs from these neighbors is relatively low (possible sneaky extra-pair copulations notwithstanding). Floaters, however, do not have a breeding partner, and have therefore a substantially higher interest in obtaining a breeding position than adults from established breeding pairs. Resident breeders are therefore expected to be more aggressive towards floaters than to members of familiar neighbors, as evidenced in Eurasian beavers (*Castor fiber*), where territorial beavers react more strongly and show more aggressive behaviors in response to scents from strange (presumed floater) than neighboring males (Rosell and Bjørkøyli, 2002). Whether residents of the opposite sex as the floater are also aggressive to the floater, or only to the same sex residents, will depend on the costs that a forceful eviction of a pair-partner has on the remaining resident. For example, if infanticide is a possible outcome after intrusion, the infanticidal sex should receive more aggression than the non-infanticidal sex. In callitrichine monkeys, where reproduction is often limited to a single female per group who may mate with several males, female infanticide occurs, but not male infanticide, (Culot et al., 2011). In line with this, female golden lion tamarins (*Leontopithecus rosalia*) aggressively chase female, but not male intruders away; on the other hand, males behave aggressively towards male, and also towards female intruders (Baker and Dietz, 1996). Furthermore, how groups react to individual floaters will depend on how they are related to the floater. If the floater is a dispersing offspring, residents may be relatively more tolerant than if it is not related, as is the case in eagle owls, where breeders are relatively tolerant towards related floaters, but very aggressive towards unknown intruders (Campioni et al., 2010, Penteriani and Delgado, 2012).

In owl monkeys, **floaters clearly pose a substantial threat to resident owl monkeys**, because floaters try to intrude into established groups, attempting to aggressively evict the same-sex resident (Fernandez-Duque and Huck, 2013). While we lack in-depth studies on inter-group encounters, which often take place at dusk or dawn and can involve quite a lot of commotion, our impression is that intense aggression between neighboring groups is rare (Fernandez-Duque, 2011, García de la Chica et al., this volume). In contrast, residents expelled by floaters can get seriously wounded and often die, and of the 12 expulsions for which we know relatively detailed circumstances, five cases resulted in wounds or limping of the former resident (Fernandez-Duque and Huck, 2013). By forcefully evicting residents, **floaters have a negative impact on the fitness of the victim, and on that of the remaining resident**. The latter, as a consequence of take-over, produces, on average, one offspring less than owl monkeys that had the same partner throughout their lives (Fernandez-Duque and Huck, 2013). This perhaps surprising finding stems from the fact that newly established pairs rarely reproduce in their first year together, while established pairs usually have an infant every year (Fernandez-Duque and Huck, 2013, Fernandez-Duque et al., 2002). While we expect that turn-over rates depend on the proportion of floaters in a population, we do not yet have sufficient data from either various populations, or over the years, to test this prediction. This suggests that **while neighboring owl monkey groups are "dear enemies", floaters that overlap the group's territory are not**. In about two thirds of the 19 cases with known circumstances, floaters settling into groups had expelled the former residents, while in a third of the cases a resident died before (Fernandez-Duque and Huck, 2013). We are not aware of a case were an adult offspring (in cases with step-parents available as breeders) became the new resident. We are also not aware of any case where a breeder from an established neighboring group took over the place of a dead neighbor. However, in one case, a former breeder ('Durazno', group D100), whose mate 'Duquesa' had died (22 Aug 2009) moved with his juvenile offspring to the neighboring group (C0, 10 Aug 2010) after the breeding male 'Cesar' of that group had disappeared (on 23 Jul 2010). This happened although a new female 'Dulcinea' had entered D100 some time after Duquesa's death (30

Dec 2009 ± 22 days). Former group D100's territory was in the following taken over by the neighboring groups and the “group” ceased to exist. This special case did not involve the expulsion of a breeder by a resident neighbor, and is the only one where a vacant breeding position was not filled by a floater. If they survive, they become secondary floaters, but they have a very low chance of becoming residents again. The only secondary floater ('Sotreta') who successfully entered a secondary breeding group, spent 7.5 months as a floater. For the remaining 10 secondary floaters, we lost contact after a mean of 4.8 (median = 5.4 months, OMD, unpubl. data). The difficulties of observing encounters between groups and floaters unfortunately prevented us so far from evaluating whether groups react differently to own dispersed biological offspring (especially in the absence of opposite-sex step-parents) and unrelated, unfamiliar floaters.

X. Mortality and reproductive success.

Due to increased risks of solitaries and aggression by established groups (sections VI & IX), floaters are likely to suffer higher losses than individuals of comparable ages in established groups. In song sparrows, for example, about half of the floaters disappeared during their second year of life, while only around 30% of territory owners of this age disappeared, and disappearances were unlikely due to further dispersal on the studied island population (Smith and Arcese, 1989). However, no study has investigated whether the extra mortality of floaters is due to increased risk of being solitary or due to inherently poorer quality, as would be suggested by the inferior genes hypothesis (section I). Moreover, the presence of floaters in a population could also affect the population-wide per-capita mortality rate, both because their own higher mortality brings the average down, and because they can pose a threat to residents, increasing their mortality risk. If floating is not explicitly an equal-fitness alternative reproductive tactic (Table 2, I.3), it can be assumed that it is a sub-optimal state and that reproductive rates of floaters are lower than those of breeders, or even non-existent (Brekke et al., 2015, but see Kempenaers et al., 2001). However, just as the attempts of floaters can impact on residents’ survival, it might also affect population dynamics more generally.

For owl monkeys, **floating is likely a sub-optimal state** that does not confer the safety benefits of living in a group, nor the opportunities to reproduce. This is reflected in the finding that the mean body mass of primary floaters (mean ± StDev. = 1185 ± 86.3 g) is 5.6 % lower than that of young adults (1255 ± 94.2 g) of a similar age range that have obtained a breeding position (Fig. 2)[1]. At the same time, the pre-dispersing subadults (mean ± StDev.

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[1] General linear model: difference floaters vs young adults: $t = 2.5$, $df = 88$, $p = 0.015$; floaters vs. subadults: ($t = 0.95$, $p = 0.35$), subadults vs young adults: $t = 1.6$, $p = 0.12$. Status of individuals was determined using a combination of age and dispersal status, thus modifying the strict classification of adults as any individual over 48 months of age (Huck et al. 2011). Individuals older than the minimum observed age of any floater (34.3 months of age) that had not yet dispersed were classified as pre-dispersed sub-adults. Individuals that had successfully dispersed to a new group were classified as

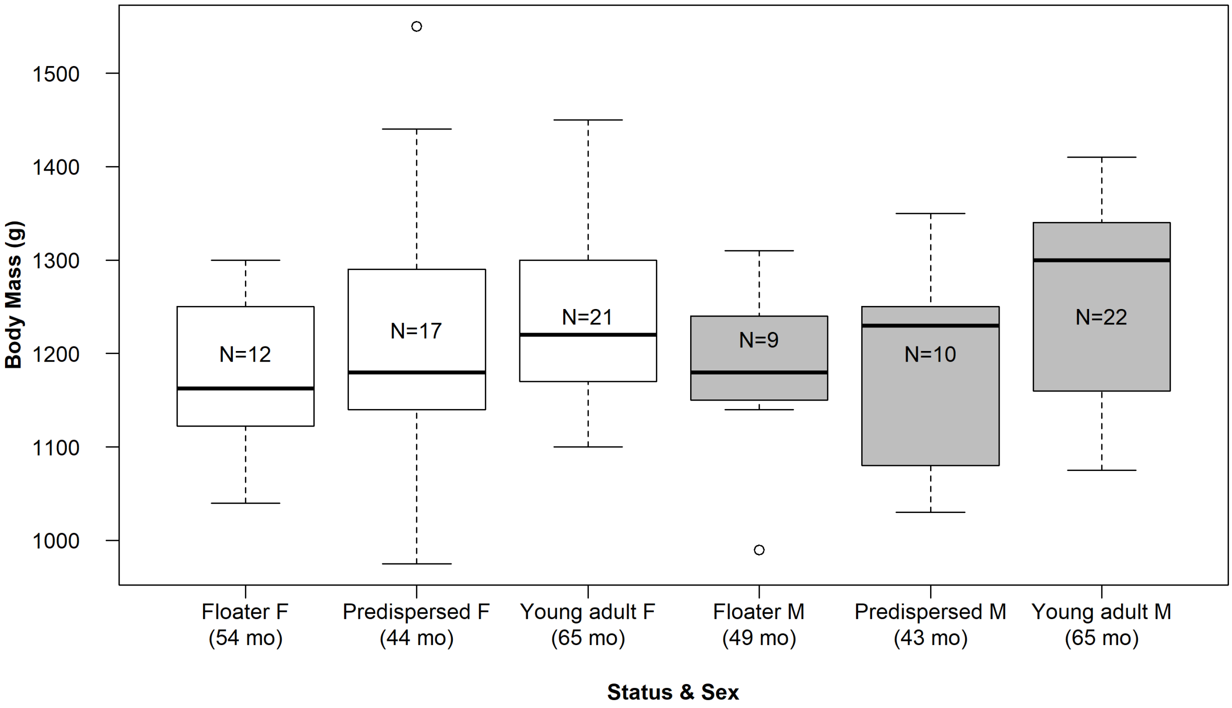

Fig 2: Body mass of female (white boxes) and male (gray boxes) owl monkeys, depending on their status. Boxes represent median and interquartile ranges (IQR). Whiskers show ranges excluding only values larger than ±1.5 times the IQR; outliers beyond this range are represented as open circles. N = number of individuals.

1214 ± 137.0 g) are rather heavier (2.4 %) than floaters, but are, in contrast to floaters, not much lighter than young adult breeders, even though the age difference is larger between subadults and young adult breeders than between floaters and young adult breeders[1]. However, it could be argued that floaters actively lose body mass in order to be more agile, thus being better able to cope with predation risk, as suggested for common teals and tufted ducks (Zimmer et al., 2011). We do not have information on muscle mass relative to body fat for owl monkeys, so cannot evaluate this possibility, but we suspect that low body mass may not be as crucial to predator avoidance strategies in owl monkeys as it seems to be for birds.

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adults. Among these, all adults not older than the oldest known age of a primary floater (76.0 months of age; this is an estimated age of an individual first identified as a floater while the oldest age for a floater of known age was 72 months) were classified as young adults. The analysis presented here compared body masses of pre-dispersed sub-adults, floaters, and young adult breeders. Thus, ages of these three classes were roughly similar, although mean ages were still different (linear regression: Floater vs. Pre-disperser: t = 3.2, df = 88, p = 0.002; Floater vs. Young adult: t = 5.5, p < 0.001). As the sexes did not differ in their body masses (t = 0.3, df = 87, p = 0.73), data for males and females were combined. Assumptions of all linear regression models were checked using residual diagnostic plots, and all indicated homogeneity of variance and normality of residuals. Details of capture procedures, aging, and body mass data collection are provided elsewhere (Fernandez-Duque and Rotundo, 2003; Juárez et al., 2011).

Place Fig. 2 approximately here

XI. Impact on population dynamics

If floaters compete with residents for breeding opportunities, attempting to forcefully evict residents will lead to higher turn-over rates amongst breeders in populations with a large floater population compared to those with only few or no floaters, all else being equal. Higher turn-over rates, interferences with breeding attempts, and fatal conflicts between floaters and residents should subsequently reduce the per-capita reproductive success (Hunt, 1998, Lenda et al., 2012). However, if a population containing floaters has reached the Moffat equilibrium (Moffat 1903, cited in Hunt, 1998), where the habitat is saturated with breeding pairs and the overall death rate equals reproduction, a per-capita reduction in reproduction due to floaters can still entail an overall positive effect on population size (Table 2, Hypothesis II.1). If only resident territory holders can breed successfully, then any mortality due to predation or disease will affect a population with a floater population (or other non-reproductive adults in group-living species) that can quickly take over vacancies less strongly than a population without such a buffer. This will be the case regardless of whether the mortality affects floaters more strongly than residents (e.g., because they are at higher risk from predation or have lower body condition (Table 2, X.1), or whether these factors affect residents to a similar degree as floaters. In that case, any mortality amongst residents would lead to a vacancy that would be filled by floaters (or other non-reproductive adults), leaving the same number of breeding pairs until the floater population is depleted (Brown, 1969). This ‘floaters-as-buffers’ effect is therefore similar to the ‘buffer effect’ as originally proposed by Kluyver & Tinbergen (1953) and further developed by Brown (1969). In that original usage, the term refers to the effect that populations of individuals settling on high quality habitats are buffered in their reproductive variance due to the presence of individuals breeding on lower quality habitats, whose reproductive variance is more variable (Sullivan et al., 2015). That is, it relates to population dynamics between breeders on high and low-quality patches. Here, we refer to an effect where essentially non-breeding mature individuals (floaters) stabilize breeding population sizes, for example against external mortality such as predation, which could be highly important for conservation considerations. This effect, however, could also for some time mask decline in absolute population numbers, if only breeders are monitored, thus delaying conservation efforts (Penteriani et al., 2011).

Additionally to these effects on population sizes, neglecting floaters could seriously underestimate the strength of selection because estimation of traits would be biased towards traits of breeders, who could have more strongly expressed ornamentation (Moreno, 2016). As our own study species is pair-living, we focus in the following discussion on pair-living species, although floaters have been described, or can be deduced (from dispersal patterns) also for many if not most group-living species (e.g. anecdotal evidence reported for equatorial sakis *Pithecia aequatorialis* and moustached tamarins *Saguinus mystax*; Fernandez-Duque et al., 2020, Löttker et al., 2004). Following Emlen and Oring's (1977) original development of the concept of the operational sex ratio, the null hypothesis for pair-living species would be that both ASR and OSR (Table 1 for definitions) are even, although there is good evidence for many bird species that sex ratios are often male biased (Donald, 2007, Moreno, 2016). However, even in species that essentially do have a balanced ASR and OSR on the level of the entire population, from an individual group's local perspective, there might be spatial and temporal imbalances due to stochastic effects of how many floaters of each sex are currently in the vicinity, the 'local OSR'. Mathematical models can help elucidate whether such stochastic effects are strong enough to impact sexual selection. Models have been used in the related, but slightly different context, of the effect of floater pressure on group formation (Port and Johnstone, 2013) and on best strategies for deciding whether to float, or not, depending on habitat quality and population density (Kokko and Sutherland, 1998). To our knowledge there have been no similar attempts at modelling the effect of the floater-dependent local and temporal variation in the local operational sex ratio on sexual selection. A similar lack of distinction in the literature between group, population and species levels of the ASR, especially in connection with the presence of floaters, has been pointed out previously (Kappeler, 2017). The temporal variation of the OSR, interacting with the ASR, and their effect on mating dynamics have been modelled theoretically (Kvarnemo and Merilaita, 2006), but only few empirical studies have addressed this. For hihis (stitchbirds) it has been suggested that reproductive success by floaters can impact the sex ratios of breeders, as well as their reproductive variance (Brekke et al., 2015).

It has been sometimes stated, that in pair-living, sexually monogamous species, sexual selection pressures should be weaker than in group-living, polygamous species, or in pair-living species with large extra-pair copulation rates (e.g., in Table 6.1 in Shuster and Wade, 2003). However, we argue that selection pressures need not be necessarily weaker, but rather simply more similar between the sexes (Fernandez-Duque and Huck, 2013, Huck et al., 2020). Thus, if the same trait is sexually selected in males (by competition amongst males for females) and females (by competition amongst females for males), no sexual dimorphism would be apparent despite potentially intense selection pressure. Furthermore, if the floaters' lack of becoming breeders is due to traits that are selected against, the impact of their phenotypes on specific sexually selected traits could be underestimated if floaters frequently move out of the study area and are thus ignored (Moreno, 2016).

We have previously hypothesized that owl monkey floater populations affect the local operational sex ratio and, thus, strength of competition and sexual selection pressures (Fernandez-Duque and Huck, 2013, Huck et al., 2020). It is difficult to examine this hypothesis empirically. Despite their direct negative impact on the fitness of the residents into whose group they intrude (section X; Fernandez-Duque and Huck, 2013), **owl monkey floaters could have a stabilizing effect on population size as a whole**. This is a suggestion for which, again, we lack data; we are left with ‘arm-chair reasoning’. With the ‘habitat saturation hypothesis’ supported and evidence of limited maximum group size, floating is an unavoidable consequence of the social organization of owl monkeys. Individuals in our population produce a mean of 6.3 offspring if they had more than one partner, and 7.9 infants if they had only one partner; this means that on average between 3-4 infants are produced for every pair (Fernandez-Duque and Huck, 2013). Mortality of reproductive adults, for example due to predation, should therefore not necessarily lead to a decrease in reproductive pairs and thus population-wide reproductive output, because, as long as there is a healthy floater population, these can take the place of the dead breeders. Monitoring and understanding the size of the floater population within a specific area could therefore give first indications of whether a population that currently seems stable could soon become at risk (if the floater population is low) or is likely to remain stable (if the floater population is large).

Conclusion and Outlook

From early on we encountered individuals that seemed to be solitary, but we did not consider them in analyses (Fernandez-Duque et al., 2001) until some time later when we realized that there was a considerable proportion of them (Fernandez-Duque and Huntington, 2002). We have made some advances in the understanding of this neglected part of the species’ social system. We now know that for both male and female owl monkeys, floating seems to be a life-stage that usually starts when they are sub-adults. While it can begin throughout the year, it is particularly common around the birth season and there is at least some aspect of enforcement by adults behind it. This is probably driven partly by food availability and, depending on the family structure, on mate competition. As floaters, the ranging patterns of floaters differ from those of groups and they seem to combine a sit-and-wait with a prospecting tactic, thus gaining information from groups while still avoiding aggression from groups. Habitat saturation, but not limited partner availability, explains why owl monkey floaters do not form their own groups. Individual floaters seem to follow different tactics, with some staying closer to their natal groups and other dispersing much further away. Likewise, the duration of this stage is flexible. Floating appears to be a sub-optimal state, without any chances of reproduction, and thus they attempt to gain breeding positions by either filling vacant breeding positions, or by forcefully creating such vacancies by expelling resident breeders. Thus, they pose a substantial threat to breeders and have a negative impact on the fitness of the victim, and likewise on that of the remaining resident.

Nevertheless, because floaters are much harder to study than established group – there are still many topics that require further attention. Difficulties of field work should not prevent us from attempting to get a better understanding of them; technological advances may open up new opportunities for studying the elusive floaters (Fernandez-Duque et al., this volume).

In the future, we need to examine secondary floaters more, as we know far less about them than primary ones. There is also a need for detailed descriptions of their behavior and activity patterns. We lack a good understanding of predation pressures on floaters (on groups as well) or what influences the duration, or range, of the floating stage. More in-depth genetic analyses will hopefully provide further insights here, and better data on the body condition of individuals is required. Methodologically, we ought to find a solution to the current sampling bias between floaters that remain in our study area and those who may employ a more transient tactic. The fate of floaters who do not become breeders is largely unknown, and this information is important to evaluate impact on population dynamics. We hope that this in-depth overview of floaters in a primate species will encourage the exchange of ideas between researchers of different taxonomic groups: let researchers on owls get inspired by owl monkeys, just as we learn from them.

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