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CHAPTER FOUR

The evolution of delayed dispersal and different routes to breeding in social birds

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1. Introduction

Many species live in groups formed by prolonged philopatry of young individuals who remain as non-reproductive subordinates and may subsequently help raise offspring (known as cooperative breeding) (Clutton-Brock & Lukas, 2012; Drobniak, Wagner, Mourocq, & Griesser, 2015; Griesser, Drobniak, Nakagawa, & Botero, 2017; Koenig & Dickinson, 2016; Taborsky, 1994). To understand the evolution of sociality, group living, and cooperative breeding, it is essential to understand why philopatric individuals delay dispersal or fail to breed independently (Ekman, Dickinson, Hatchwell, & Griesser, 2004; Hatchwell, 2009; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992; Walters, Copeyon, & Carter, 1992; Walters, Doerr, & Carter, 1992; Wiley & Rabenold, 1984). However, this question can only be answered if the costs and benefits of philopatry are compared to those of alternative options, in particular leaving to roam through the population in search of a breeding territory.

Three main hypotheses have been proposed to explain delayed dispersal (Koenig et al., 1992). (i) The ecological-constraints hypothesis (Emlen, 1982; Selander, 1964) predicts that ecological or demographic constraints, such as shortage of mates or suitable breeding vacancies (habitat saturation), combined with the high costs associated with finding these, inhibit dispersal to an independent breeding position until a suitable vacancy becomes available. By building upon the ecological-constraints hypothesis, the (ii) life-history hypothesis makes the broad prediction that when adult mortality is low (as is often the case in social species; Beauchamps, 2014), individuals postpone independent breeding until a high-quality territory becomes available because high life expectancy (and therefore low relative value of current vs future reproduction) makes it worthwhile to wait (Arnold & Owens, 1998; Covas & Griesser, 2007; Ekman et al., 2004; Hatchwell & Komdeur, 2000; Mourocq et al., 2016; Ricklefs, 1974). Together, these two hypotheses may explain why individuals delay independent breeding, but they do not necessarily provide an explanation for why individuals stay in their natal territory. For this reason, the (iii) benefits-of-philopatry hypothesis (Stacey & Ligon, 1987, 1991) was proposed, predicting that individuals delay dispersal when the survival and reproductive benefits (their own reproduction, and indirect benefits from helping raise relatives in cooperatively breeding species) in a natal territory exceed those of dispersal (Ekman, Bylin, & Tegelström, 2000; Griesser, Nystrand, & Ekman, 2006; Kingma, Hall, & Peters, 2011;

Kingma, Santema, Taborsky, & Komdeur, 2014; Kokko & Ekman, 2002; Richardson, Burke, & Komdeur, 2002). It is now recognized that to create a comprehensive understanding of delayed dispersal (and thus the evolution of sociality, group living and cooperative breeding), these three hypotheses need to be combined by determining how various environmental, demographic, social, intrinsic, and genetic factors affect the costs and benefits of delayed dispersal (Covas & Griesser, 2007; Ekman et al., 2004; Hatchwell, 2010; Hatchwell & Komdeur, 2000; Koenig, Dickinson, & Emlen, 2016; Koenig et al., 1992; Walters, Doerr, & Carter, 1992). Despite much conceptual, theoretical and empirical study, however, still no consensus has been reached (e.g., Covas & Griesser, 2007; Ekman, 2006; Ekman et al., 2004; Hatchwell, 2009, 2016; Hatchwell & Komdeur, 2000; Komdeur & Ekman, 2010; Nelson-Flower, Wiley, Flower, & Ridley, 2018; Shen, Emlen, Koenig, & Rubenstein, 2017).

We argue that one reason for the lack of consensus about the evolution of delayed dispersal is perhaps partly that the term "delayed dispersal" implies a disproportionately heavy focus on the "why stay and not breed or float" component—i.e., the period that individuals spend as subordinate. However, while delayed dispersal may be beneficial in the short term (reviewed in, e.g., Cockburn, 1998; Covas & Griesser, 2007; Ekman, Baglione, Eggers, & Griesser, 2001; Ekman et al., 2004; Koenig et al., 1992, 2016; Koenig, Shen, Krakauer, & Haydock, 2009; Shen et al., 2017; Walters, Copeyon, & Carter, 1992; Walters, Doerr, & Carter, 1992), in order for selection to act on it, individuals need to ultimately obtain fitness, and the largest part of their fitness most likely derives from breeding independently later in life (Clutton-Brock, 2002; Koenig & Mumme, 1987; Richardson et al., 2002; Stacey & Ligon, 1987). Such fitness later in life may depend on the circumstances and decisions made earlier in life. Thus, to explain the factors driving delayed dispersal, the short-term costs and benefits (those while waiting or searching for an independent breeding position), as well as the long-term costs and benefits (those once a breeding position is obtained) should be assessed. Currently, we lack a clear overview, and empirical assessments, of how individuals in social species can optimize their chances to breed independently and what determines the success of all potential options.

1.1 What are the potential routes to obtaining an independent breeding position?

A unified understanding of delayed dispersal may be hampered by the fact that understanding the fitness consequences of dispersal requires not only

considering why individuals stay, but also the specific route that they take from their natal territory to an eventual breeding territory. Since social species are characterized by strong competition over limitedly available suitable, or high quality, areas or partners, the probability of obtaining a breeding position is generally low. First, expelling established breeders to take over a breeding position is rare (although it does occur; Raihani, Nelson-Flower, Golabek, & Ridley, 2010; Walters, Doerr, & Carter, 1988; Zahavi, 1990), either because breeders are dominant over subordinates or because the group can evict intruders that aim to take over a breeding position (Woolfenden & Fitzpatrick, 1977). Second, as breeding habitat in social species is often saturated, individuals can rarely set up a new territory in unoccupied habitat (but see Goldizen, Putland, & Robertson, 2002; and Section 2.1.2). Thus, subordinates usually rely on vacancies to become a breeder (Pasinelli & Walters, 2002), which they can either search for in the wider population, or wait for in the natal territory until a same-sex breeder disappears from the natal or a nearby territory (Raihani et al., 2010). Vacancies may be filled on a first-come-first-served basis (e.g., Eikenaar, Richardson, Brouwer, Bristol, & Komdeur, 2009) but can also be strongly contested (Barve, Hagemeyer, et al., 2020; Barve, Lahey, Brunner, Koenig, & Walters, 2020; Hannon, Mumme, Koenig, & Pitelka, 1985; Zack & Rabenold, 1989).

Remarkably little is known about the alternative strategies that lead to independent breeding, or how these affect fitness (Koenig et al., 2016). Different routes to find, assess and occupy vacancies (Kokko & Ekman, 2002) may be associated with specific costs and benefits (Ekman et al., 2004; Koenig et al., 1992; Table 1). If subordinate individuals remain in

Table 1 Overview of potential benefits of five routes to an independent breeding position (see Section 2 and below table for a detailed description).

	Inheritance	Shifting	Budding	Prospecting	Floating
(A) Benefits while being a subordinate					
Access to extra-group mating	±	±	±	+	+
Access to within-group mating	+	+	+	±[a]	0
Benefits of helping	+	+	+	±[a]	0
Reduced predation	+	+	+	−[b]	−[b]

Table 1 Overview of potential benefits of five routes to an independent breeding position (see Section 2 and below table for a detailed description).—cont'd

	Inheritance	Shifting	Budding	Prospecting	Floating
Reduced conspecific competition and aggression	+	±	±	−[b]	−[b]
Better condition	+	+	+	±[b]	−[b]
Higher survival	+	+	+	±[b]	−[b]
Parental support in establishing a territory	+	+	+	0	0
Likelihood of finding vacancy	−	±	±	+	+
Familiarity with area	+	±	±	−	−
(B) Benefits after position obtained					
Long breeding tenure	−	±	±	+	+
Good quality breeding territory	±	±	−[c]	+	+
Kin support or reciprocal altruism	+	+	+	0[b]	0[b]
Less related partner	−	±	+[d]	+	+
Familiarity with the area and partner	+	±	±	0	0

[a]Although prospectors may help in their natal territory, they may trade off time and energy between prospecting and helping (Young, Spong, & Clutton-Brock, 2007). Similarly, within-group mating may be traded off against prospecting.
[b]The costs and benefits may be altered when individuals can prospect or float in coalitions (see Section 2.2.2).
[c]Budded territories may initially be of poor quality, because they are smaller, and may collapse (see Komdeur & Edelaar, 2001a; Legge & Cockburn, 2000).
[d]Although budders probably live in kin clusters, they usually attract an unrelated partner (Cockburn, Osmond, Mulder, Green, & Double, 2003; Hidalgo Aranzamendi, Hall, Kingma, Sunnocks, & Peters, 2016; Komdeur & Edelaar, 2001a; Woolfenden & Fitzpatrick, 1978, 1990).
These benefits can be obtained (A) as subordinate, while waiting or searching for a vacancy, or (B) as breeder, after individuals have obtained an independent breeding position (see Fig. 2). The predicted benefits are classified as relatively large (+), intermediate (±), non-existent (0) or negative (−). Prospectors and floaters both engage in extra-territorial movement, whereas strictly philopatric individuals can obtain a breeding position via inheritance, shifting and budding. For most, but not all, benefits there are conspicuous differences between philopatric and dispersing individuals, in line with the foundation of the benefits of philopatry hypothesis. However, the benefits for philopatric individuals can also vary substantially depending on what route to breeding (inheritance, shifting, budding or prospecting) is applied, and these differences take effect before or after they have established a breeding position. Note that the magnitude and the importance of each of these benefits may differ between species, depending the relative importance of various other ecological and social factors that may have an effect simultaneously. Individuals may also disperse to a subordinate position in a non-natal territory, but we have not included the relative benefits of such staging here since stagers can eventually obtain a breeding position via each of the five listed routes to breeding (note, however, that benefits for subordinate staging individuals to large extent resemble those of philopatric individuals).

the natal group, they may subsequently *inherit* the breeding position (Woolfenden & Fitzpatrick, 1978; Fig. 1A), *bud off* a part of the territory to form a new breeding territory (Komdeur & Edelaar, 2001a; Woolfenden & Fitzpatrick, 1978; Fig. 1B) or *shift* to a breeding position arising in a neighboring territory (Kokko & Ekman, 2002; Zack, 1990; Fig. 1C). Subordinates may also assess the availability and quality of breeding territories over an extended area through temporary trips from their resident territory ("*prospecting*"; Doolan & Macdonald, 1996; Young & Monfort, 2009; also referred to as "*stay-and-foray*"; Brown, 1987; Koenig et al., 1992; Kokko & Ekman, 2002; Reed, Boulinier, Danchin, & Oring, 1999; Fig. 1D). Alternatively, individuals may permanently leave their natal territory and move around until they find a breeding vacancy ("*floating*"; Ridley, Raihani, & Nelson-Flower, 2008; Zack & Stutchbury, 1992; Fig. 1E). These routes directly lead to independent breeding, but individuals may also permanently leave their natal territory and engage in "*staging*" (also referred to as "*staging-post dispersal*"; Cockburn et al., 2003; Fig. 1F), where they join another group as a subordinate, from where they can acquire a breeding position. While several or all of these routes commonly occur within most social species (see below), comparison of potential routes to independent breeding has received limited empirical attention. Thus, although the effects of various routes to breeding have been described (e.g., Ekman et al., 2004; Koenig et al., 1992), we argue that whether, how, and under what circumstances individuals can obtain a breeding position must be considered more explicitly in order to make more comprehensive inferences about the evolution of delayed dispersal.

1.2 Aims of this review

In order to guide and inspire future work to unravel the evolutionary drivers of (delayed) dispersal, our aim is to (i) explicitly define all routes to independent breeding, (ii) consider the factors potentially contributing to costs and benefits of each of these potential routes and thereby (iii) provide a comprehensive framework for future studies. For simplicity, we mainly focus on social birds (both cooperative and non-cooperative group-living species, where subordinates respectively do and do not help dominant individuals in their reproduction; Cockburn, 1998; Drobniak et al., 2015; Ekman, 2006), but many of the routes to breeding and their underlying mechanisms are probably similar in other taxa (see Mares, Bateman, Clutton-Brock, & Young, 2014; Jungwirth, Walker, & Taborsky, 2015, for examples) and, to some degree, also in non-social species (Reed et al., 1999).

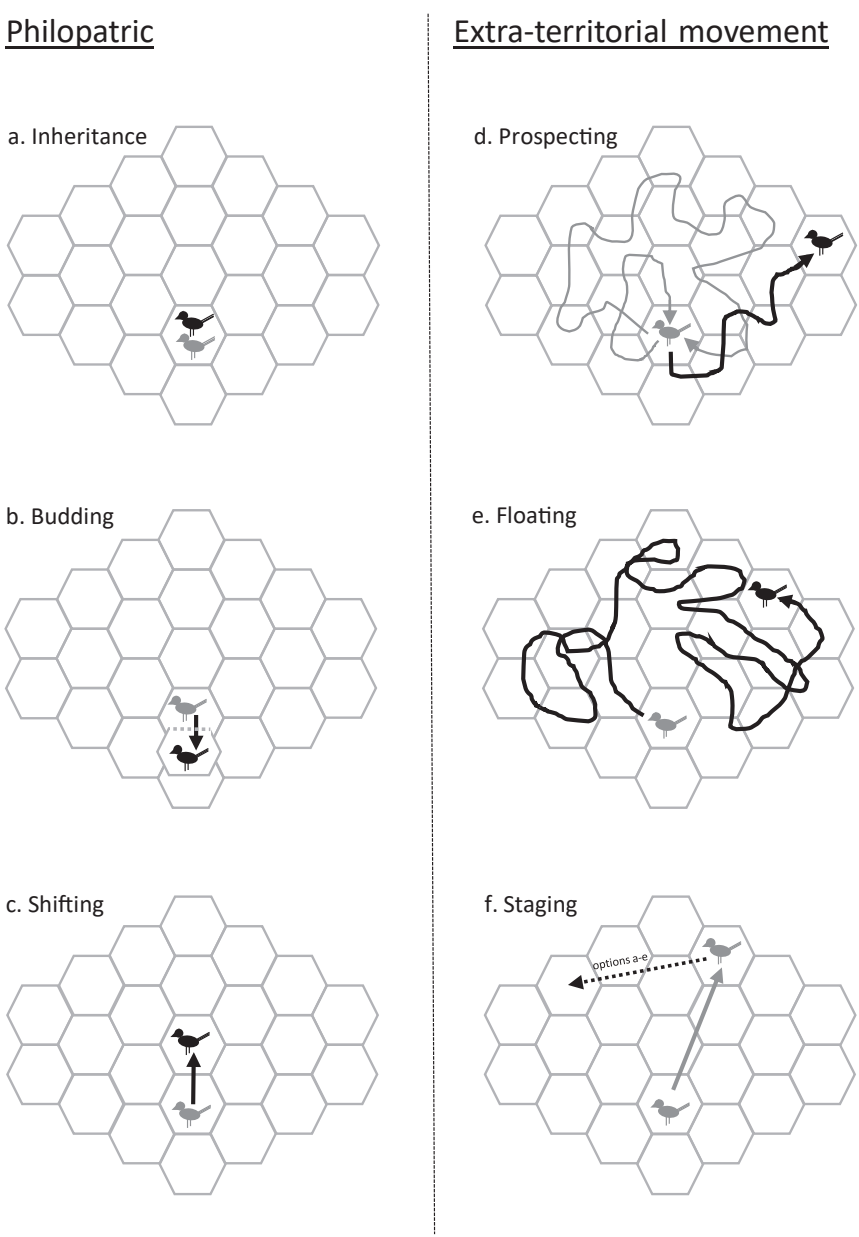

Fig. 1 A schematic overview of the different routes that subordinate individuals (depicted as gray bird) can follow to become an independent breeder (black bird) in a territory (depicted as hexagons). Philopatric individuals delay dispersal and can wait to (A) *inherit* the breeding position in their natal territory when the same-sex breeder disappears, (B) *bud off* part of their natal and surrounding territories to establish

(Continued)

In Section 2, we review the existing studies of each different route to breeding within and across species. For each route we describe the processes, summarize their relative occurrence across species, and outline the proximate drivers of different routes to breeding. In Section 3, we compare the costs and benefits of different routes, followed by recommendations for future work in Section 4. Throughout, we highlight that it is particularly important to realize that circumstances in early and late life (e.g., as subordinate or breeder) may have different effects on the fitness of individuals, and that fitness is built up from different components (Koenig et al., 1992; see Fig. 1). To illustrate this, we create a framework based on the premise that the fitness obtained by either delayed dispersal (and its associated routes to independent breeding) or floating consists of four major components (Fig. 1; Section 3): (1) subordinate fitness, consisting of indirect benefits obtained from improving reproduction of relatives and direct access to reproduction by subordinates in their natal territory, (2) survival probability while searching or waiting for a position (survival benefits of philopatry vs survival costs of floating), (3) duration of breeding tenure, and (4) relative quality of an acquired breeding position (determining reproductive success). Based on this framework, we will outline reasons why assessing each of the different routes to breeding, and the differences between these, is important for empirical and theoretical work aimed at understanding what factors drive delayed dispersal.

2. Routes to independent breeding: Benefits and costs

In this section we describe the characteristics of each route to independent breeding. We describe costs and benefits specific to each route (both theoretical and demonstrated empirically), and make inferences about what circumstances select for each of these routes. Due to their distinctive nature, we conceptually separate the routes that do not (Section 2.1) and that do

Fig. 1—Cont'd a new territory, or (C) *shift* to a neighboring vacancy. Individuals may also engage in extra-territorial movement in search of a vacancy, by (D) temporary *prospecting* trips (after which they can return to their natal territory if they do not find a territory (gray arrows) or settle as breeder in a vacancy (black arrow)) or by (E) permanently leaving their natal territory to *float* through the population. In some species, individuals leave their natal territory to (F) *stage* as subordinate in another territory (either the neighboring territory or further away after a period of prospecting or floating); as indicated by the dotted arrow, stagers may subsequently obtain a breeding position by following either of the abovementioned routes (A–E).

(Section 2.2) require movement outside the resident territory ("extra-territorial" movement). Subsequently, we discuss an intermediate step, by which subordinates disperse to a subordinate position in another group ("staging"; Section 2.3).

Note that throughout this review we treat the different routes to independent breeding as separate concepts. However, they are by no means exclusive; several routes to breeding are often present within a species or adopted by single individuals attempting to obtain a breeding position (Walters, Cooper, Daniels, Pasinelli, & Schiegg, 2004).

2.1 Independent breeding via natal philopatry

Individuals can follow three routes to independent breeding without moving outside their natal territory while waiting for a breeding position (Fig. 1A–C): (i) acquire direct access to a vacancy that appears when a breeder of the same sex on the natal territory disappears (*inheritance*), (ii) bud off part of their natal territory to form a new, independent place to breed (*budding*) or (iii) directly move to a vacancy in an adjacent territory (*shifting*). Regardless of which route philopatric individuals eventually follow, all these routes are initially preceded by similar benefits of philopatry while waiting (see Table 1). We will not consider the benefits of philopatry in detail here since subordinate reproduction, indirect fitness and survival benefits of philopatry have all been excellently reviewed and discussed elsewhere (e.g., Cockburn, 1998; Covas & Griesser, 2007; Ekman et al., 2001, 2004; Griffin & West, 2003; Koenig et al., 1992, 2009, 2016; Riehl, 2017; Shen et al., 2017; Walters, Copeyon, & Carter, 1992; Walters, Doerr, & Carter, 1992) and will be touched upon in Section 3 (and Fig. 2). Instead, we focus in this section mainly on the likelihood that individuals can find, fill and survive in a position (together accumulating to breeding tenure duration; component 3 in Fig. 2) and how the relative quality of the acquired position affects reproduction (component 4 in Fig. 2), since those fitness components have received less attention and are directly relevant for assessing the different routes to breeding applied by philopatric individuals. We highlight here first some generic benefits that apply to all three philopatric routes to breeding, before addressing the aspects unique to each separate route in Sections 2.1.1–2.1.3.

General advantages of philopatry: Remaining on a natal territory may allow resident subordinates to opportunistically detect and capitalize faster on vacancies that arise in their immediate environment than those who disperse to search for a vacancy. This may especially be important in species with a

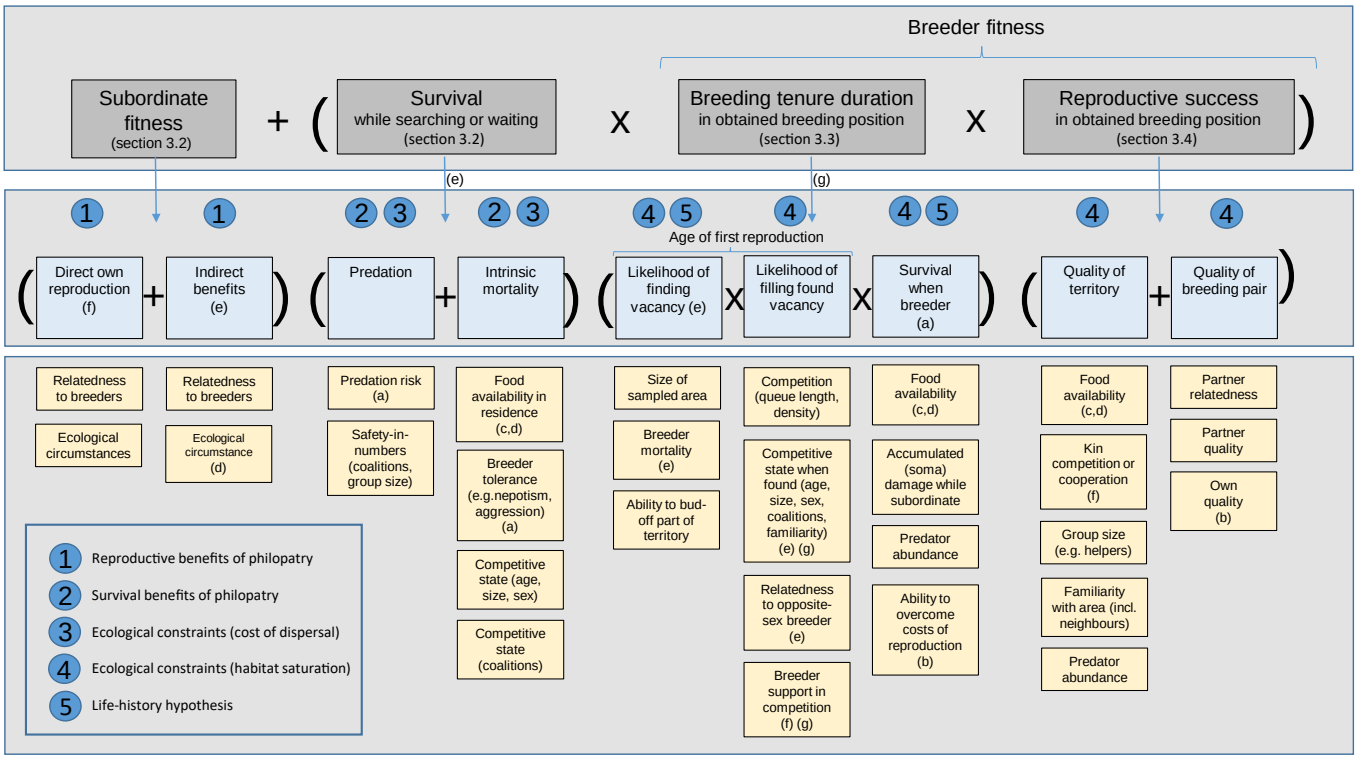

Fig. 2 See figure legend on opposite page.

first-come-first-served mechanism of territory occupation, as in for example the Seychelles warbler (*Acrocephalus sechellensis*; see Eikenaar et al., 2009). However, even in species with strong competition for breeding vacancies (see, e.g., Barve, Lahey, et al., 2020 and Rabenold, 1990 for descriptions of physical contests over vacancies), individuals from the local area may be more successful in filling the vacancy than individuals from further away. For example, up to 10 subordinate stripe-backed wrens *Campylorhynchus nuchalis*, compete for days over experimentally-created, high-quality vacancies and these contests are much more likely to be won by local individuals (Rabenold, 1990; Zack & Rabenold, 1989). The exact reason for the latter is unclear, but the fact that local individuals are more willing to engage in fights suggests that such individuals might have a home advantage in competition (see, e.g., Kemp & Wiklund, 2004), for example, because they are supported by local and familiar individuals or because they have knowledge of the local environment, including the presence of food, predators and conspecifics (Zack & Stutchbury, 1992).

Once philopatric individuals gain a local breeding position, further benefits may derive from reciprocal altruism, i.e., peaceful social bonds with familiar or related neighboring individuals that were already formed as a subordinate. According to this hypothesis, genetically more similar or socially

Fig. 2 A schematic overview of the four components (gray boxes) that combine to individuals' life-time fitness: the fitness obtained as subordinate, and the survival probability until obtaining a breeding position multiplied by breeder fitness (which is the product of the duration of breeding tenure and the annual reproductive success in the breeding position). Each components is composed of several elements (blue boxes), which can be affected by a set of environmental, social or intrinsic potential determinants (yellow boxes). All of the components, elements, and determinants may vary between the various routes of breeding that subordinate individuals can apply or have applied to obtain an independent breeding position, and have been incorporated in established hypotheses of delayed dispersal (benefits-of-philopatry (blue circles 1 and 2), ecological-constraints (blue circles 3 and 4), and life-history hypothesis (blue circle 5)). Combining these hypotheses in this framework provides the opportunity to integrate all factors that are predicted to determine the ultimate costs and benefits of all potential routes to independent breeding. Letters between parentheses refer to studies on social species in which the effect of specific elements and/or determinants on life-time fitness were compared between different routes to breeding (a: Siberian jay (Ekman, Bylin, & Tegelström, 1999); b: green woodhoopoe (Hawn, Radford, & du Plessis, 2007); c: Seychelles warbler (Komdeur, 1992; Komdeur & Edelaar, 2001a); d: acorn woodpecker (Stacey & Ligon, 1987, 1991); e: red-cockaded woodpecker (Walters, Copeyon, & Carter, 1992; Walters, Doerr, & Carter, 1992); f: Mexican jay (Brown & Brown, 1984); g: Florida scrub-jay (Fitzpatrick & Bowman, 2016)).

more familiar neighbors are less competitive and aggressive over territory borders and may be more cooperative in for example predator repellence (see Ridley, Yu, & Sutherland, 2005, for a theoretical approach). Empirical tests of this hypothesis are rare, but genetic clustering at the population level is a common characteristic of social species (reviewed in Hatchwell, 2010), suggesting that such benefits could be widespread (but note that kin clustering could also result in competition with kin for resources; Hamilton & May, 1977; Hewett Ragheb & Walters, 2011; Kokko & Ekman, 2002; Lambin, Aars, & Piertney, 2001; Pasinelli & Walters, 2002; Sorato, Griffith, & Russell, 2016). In support of the reciprocal altruism hypothesis, Seychelles warblers were shown to fight less with related and familiar neighbors, resulting in better condition (Bebbington et al., 2017). Such advantages may result in enhanced survival (and thus longer breeding tenure) and reproductive quality of the position because the time and energy saved can be allocated to reproduction. Philopatric individuals might also have the additional advantage that detailed knowledge of the local environment, including prior assessment of the quality of territories in the near vicinity of the natal territory may also enhance reproductive quality of the position for philopatric individuals (Fig. 2) (Brown & Brown, 1984; Ekman et al., 1999; Zack, 1990), may allow them to make better-informed decisions for choosing to settle in a territory or not (see Forero, Donázar, & Hiraldo, 2002 for a non-social species example).

Thus, because local breeding positions are situated in a familiar environment or environment consisting of relatives, philopatric individuals obtaining a position through inheritance, budding or shifting can benefit in various ways from improved chances of obtaining a breeding position and from breeding in a relatively high-quality breeding position (Fig. 2).

2.1.1 Territory inheritance via philopatry

In most social species, a proportion of philopatric individuals inherit the breeding position in their natal territory when the existing same-sex breeder in that territory dies or disperses (Table 2 and Fig. 1A). Although territory inheritance has been recognized as a benefit of philopatry and route to independent breeding (see, e.g., theoretical models by Kokko & Ekman, 2002; Kokko & Sutherland, 1998; Pen & Weissing, 2000a, 2000b), its importance appears underestimated in previous accounts of delayed dispersal (e.g., Ekman et al., 2004; see also Downing, Griffin, & Cornwallis, 2018). In fact, our overview shows that territory inheritance is a relatively important route to breeding (Table 2: in 28 species on average 16% of females and 26% of

Table 2 All potential routes to independent breeding are common, with females usually more likely to prospect and/or float, as shown in this overview of studies that quantified how individuals obtained their first breeding position, distinguishing philopatric routes (inheritance of the natal territory, shifting and budding) from those requiring extra-territorial movement (breeding position more than one territory from the natal territory).

			Routes to independent breeding (% of positions obtained)			
Species	**Breeding system**	**Sex**	**Inheritance of natal territory**	**Shift (budding)**	**Prospect/float (>1 territory)**	**References**
Red-cockaded woodpecker	Singular	Females	3	28	69	Walters et al. (1988)
Leuconotopicus borealis		Males	27	25	48	Daniels and Walters (2000a)
Laughing kookaburra	Singular	Females	0	? (38)[a]	?	Legge and Cockburn (2000)
Dacelo novaeguineae		Males	0	? (38)[a]	?	
Stripe-backed wren	Singular	Females	4	40	56	Rabenold (1990)
Campylorhynchus nuchalis		Males	53	29	18	
Bicolored wren	Singular	Females	47[b]	36[b]	17[b]	Austad and Rabenold (1986)
Campylorhynchus griseus		Males	17[b]	24[b]	59[b]	
Florida scrub-jay	Singular	Females	0	28 (6)	66	Woolfenden and Fitzpatrick (1984)
Aphelocoma coerulescens		Males	13	19 (47)	21	
Superb fairy-wren	Singular	Females	0	4 (0)	96	Cockburn et al. (2003), Cockburn, Osmond, Mulder, and Green (2008)
Malurus cyaneus		Males	39	38 (21)	2	
Purple-crowned fairy-wren	Singular	Females	8	4 (1)	87	Hidalgo Aranzamendi et al. (2016)
Malurus coronatus		Males	24	34 (11)	31	
Blue-breasted fairy-wren	Singular	Females	0	<15[c]	>85[c]	Rowley and Russell (2002)
Malurus pulcherrimus		Males	15	<47[c]	>38[c]	

Continued

Table 2 All potential routes to independent breeding are common, with females usually more likely to prospect and/or float, as shown in this overview of studies that quantified how individuals obtained their first breeding position, distinguishing philopatric routes (inheritance of the natal territory, shifting and budding) from those requiring extra-territorial movement (breeding position more than one territory from the natal territory).—cont'd

			Routes to independent breeding (% of positions obtained)			
Species	**Breeding system**	**Sex**	**Inheritance of natal territory**	**Shift (budding)**	**Prospect/float (>1 territory)**	**References**
Green woodhoopoe	Singular	Females	47[d]	37	16	Ligon and Ligon (1990)
Phoeniculus purpureus		Males	27[d]	61	12	
Pied babbler	Singular	Females	13[e]	?	?	Raihani et al. (2010)
Turdoides bicolor		Males	21[e]	?	?	
Rufous Vanga	Singular	Females	0	?	?	Eguchi, Yamagishi, Asai, Nagata, and Hino (2002)
Schetba rufa		Males	5	79[f]	16	
Carrion crown	Singular	Females	0	?	?	Baglione and Canestrari (2016)
Corvus corone		Males	0	?	?	
White-browed sparrow-weaver	Singular	Females	12	40	48	Harrison, York, and Young (2014)
Plocepasser mahali		Males	19	15	67	
Rufous treecreeper	Singular	Females	13	<40[c]	>47[c]	Luck (2001)
Climacteris rufa		Males	7	<57[c]	>36[c]	
Karoo scrub-robin	Singular	Females	3	7	90	Ribeiro, Lloyd, Feldheim, and Bowie (2012)
Cercotrichas coryphaeus		Males	9	71	20	
Seychelles warbler	Singular +joint	Females	2	12 (0)	86	Eikenaar, Komdeur, and Richardson (2008) and Eikenaar et al. (2009)

Acrocephalus sechellensis		Males	4	29 (6)	61	
Arabian babbler	Singular + joint	Females	4	68	28	Zahavi (1990)
Turdoides squamiceps		Males	31	52	17	
Groove-billed anis	Joint	Females	2	<6	>92	Koford, Bowen, and Vehrencamp (1990)
Crotophaga sulcirostris		Males	22	<34	>44	
Acorn woodpecker	Joint	Females	20[g]	14	66	Koenig, Hooge, Stanback, and Haydock (2000)
Melanerpes formicivorus		Males	60[g]	15	25	
Red-winged fairy-wren	Singular (+plural[h])	Females	41[i]	30 (0)[i]	29[i]	Russell and Rowley (2000)
Malurus elegans		Males	76[i]	17 (2)[i]	5 9	
Splendid fairy-wren	Singular + plural	Females	39	43	18	Russell and Rowley (1993)
Malurus splendens		Males	61	26	13	
Tasmanian native hen	Singular + plural	Females	38	54	8	Goldizen et al. (2002)
Tribonyx mortierii		Males	12	57	31	
Mexican Jay	Plural	Females	68	32	0	Brown and Brown (1984)
Aphelocoma wollweberi		Males	71	29	0	
Galápagos mockingbird	Plural	Females	47	18	35	Curry and Grant (1990)
Mimus parvulus		Males	62	31	7	
Superb starling	Plural	Females	5	?	?	Rubenstein (2016)

Continued

Table 2 All potential routes to independent breeding are common, with females usually more likely to prospect and/or float, as shown in this overview of studies that quantified how individuals obtained their first breeding position, distinguishing philopatric routes (inheritance of the natal territory, shifting and budding) from those requiring extra-territorial movement (breeding position more than one territory from the natal territory).—cont'd

			Routes to independent breeding (% of positions obtained)			
Species	**Breeding system**	**Sex**	**Inheritance of natal territory**	**Shift (budding)**	**Prospect/float (>1 territory)**	**References**
Lamprotornis superbus		Males	39[j]	?	?	
Brown Jay	Plural	Females	28	>62	<10	Williams and Rabenold (2005)
Cyanocorax morio		Males	12	>83	<5	
Siberian Jay	Family living	Females	0	<26	>74	Ekman et al. (2001)
Perisoreus infaustus		Males	0	60	40	
Western slaty antshrike	Family living	Females	0[k]	11[k]	89[k]	Tarwater (2012)
Thamnophilus atrinucha		Males	0[k]	11[k]	89[k]	

[a]Shifting unknown but 39% of position is obtained by budding (sexes combined).
[b]Average of two populations (Austad & Rabenold, 1986).
[c]Only individuals from outside the study area were included as "Prospectors/floaters." The percentages for "shifting" presumably also includes some individuals that came from further than just the neighboring territory (Luck, 2001; Rowley & Russell, 2002).
[d]Estimate of inheritance 58% in another study (for sexes combined; Hawn et al., 2007).
[e]Values slightly higher in Nelson-Flower, Hockey, O'Ryan, and Ridley (2012).
[f]May include budding (but unclear; Eguchi et al., 2002).
[g]In another population of acorn woodpeckers fewer individuals inherited a territory (Koenig & Stacey, 1990).
[h]Plural breeding is relatively rare in red-winged fairy-wrens (Russell & Rowley, 2000).
[i]Percentages based on juveniles ringed in the study area (Russell & Rowley, 2000).
[j]Percentage of males breeding in their natal territory is stated "*almost certainly an underestimate*" (Rubenstein, 2016).
[k]No sex-specific values given, but no significant differences between males and females.
Staging was not included since it is difficult to classify and rarely quantified in individual studies of the routes to breeding: staging is an intermediate strategy between natal philopatry and obtaining a breeding position through subsequent "inheritance," budding, shifting, prospecting or floating. Only territorial species were included (excluding colonial species, species where helpers are juveniles hatched in the same season, and species where helpers redirect care). Percentages are separated per sex, and the breeding system of each species is given. Note that the percentages for all routes to breeding are not available for all species (as indicated by question marks). Moreover these estimates only include individuals that survived and could be detected in the respective studies; since prospecting and floating individuals have a higher likelihood to die in the process of dispersing (Table 3) and may have gone undetected after leaving the study area, the percentage of individuals that prospect/float (and obtain a position this way) is likely an underestimation, whereas, conversely, the percentages of individuals that inherit, bud and shift may in reality be slightly lower.

males inherit a territory; ranging from 0% to 76% of individuals overall). Nonetheless, empirical studies into the costs and benefits of territory inheritance are somewhat limited (Table 2).

Although direct empirical evidence is rare, inheritance has been suggested to offer benefits unique to breeding in the natal territory in addition to the benefits of obtaining a local position outlined above. For example, familiarity with successful nesting locations and with their partner may reduce or obviate the frequently observed lower success of first-time breeders or unfamiliar mates (see, e.g., Naves, Cam, & Monnat, 2007 and references cited therein), and thereby increase life-time success. More broadly, breeders are also thought to encourage offspring to remain philopatric so they can bequeath the territory to a close relative (as suggested by Brown, 1974, 1987; Brown & Brown, 1984), and such a mutual benefit for both breeders and subordinates may strongly select for delayed dispersal (see Brown, 1987; Lindström, 1986; for parental facilitation models; but see also chapter 9 in Koenig & Mumme, 1987). Following similar logic, subordinate group members may gain indirect benefits from supporting a higher-ranked relative who competes to fill a breeding vacancy in their territory; this way, individuals may experience less aggression from group members when they attempt to obtain a breeding position at home. Moreover, cooperation from group members may also benefit a former subordinate that has become the breeder: the group-augmentation theory proposes that individuals benefit from helping to raise non-descendent offspring in a natal territory if they can subsequently inherit the territory and if the offspring they helped raise become their future helpers (Kingma, 2017; Kingma et al., 2014; Kokko, Johnstone, & Clutton-Brock, 2001; Ligon & Ligon, 1978). Direct evidence that delayed reciprocal benefits of group augmentation are an important driver of delayed dispersal is lacking so far (Kingma et al., 2014) but it is supported by the observation that subordinate male stripe-backed wrens obtain a territory with a larger number of helpers if they inherit the territory compared to individuals that disperse (Piper, Parker, & Rabenold, 1995). In addition, interspecific comparisons of cooperatively breeding birds show that the prospects of inheritance predict how much subordinates invest in helping behavior (Downing et al., 2018; Kingma, 2017; see also Kingma et al., 2011), suggesting that territory inheritance may also select for delayed dispersal in the first place.

Although territory inheritance can clearly have several unique benefits, theoretical and empirical work highlights that certain restrictions and limitations apply (e.g., Kokko & Ekman, 2002). First, breeding opportunities in the natal territory are limited and depend on the rate of mortality of breeders

(Lindström, 1986). This may lead to long waiting periods (Eikenaar, Richardson, Brouwer, & Komdeur, 2007; Yaber & Rabenold, 2002) and consequently relatively short breeding tenure duration for subordinates (Cant & English, 2006; Kokko & Johnstone, 1999), but this is not always the case (Russell & Rowley, 1993). Second, individuals may also have to wait longer when the queue of same-sex individuals for inheritance is longer. In many social species, a stable and hierarchical queue exists (e.g., Cockburn et al., 2008; Ekman et al., 2001; Kingma et al., 2011, 2014; Yaber & Rabenold, 2002; Zahavi, 1990) based on differences in age (older individuals are head of the queue; e.g., Cockburn et al., 2008), condition (Hewett Ragheb & Walters, 2011; Pasinelli & Walters, 2002), or levels of ornamentation (Fan et al., 2018). Indeed, a theoretical model by Kokko and Ekman (2002) shows that when queues become too long, young individuals should disperse to search for an alternative breeding position, as confirmed in empirical studies on brown jays (*Cyanocorax morio*; Williams & Rabenold, 2005), stripe-backed wrens (Piper et al., 1995) and (male) pied babblers (*Turdoides bicolor*; Nelson-Flower et al., 2018). Third, individuals who inherit the territory and pair with the remaining breeder after the same-sex breeder disappears may have a high likelihood of engaging in an incestuous pairing (Nichols, 2017). In some species this is not the case, either because of active incest avoidance (e.g., Arabian babblers (*Turdoides squamiceps*; Zahavi, 1990), Florida scrub-jay (*Aphelocoma coerulescens*; Woolfenden & Fitzpatrick, 1990), laughing kookaburras (*Dacelo novaeguineae*; Legge & Cockburn, 2000), acorn woodpeckers (*Melanerpes formicivorus*; Koenig & Stacey, 1990), pied babblers (Nelson-Flower et al., 2012); see also Nichols, 2017) or because high mortality rates of breeders lead to low probability of incestuous pairing (green woodhoopoes (*Phoeniculus purpureus*; Ligon & Ligon, 1990); see also table 3 in Cockburn, 1998). In several other species, incestuous pairings do occur (e.g., Seychelles warblers (Eikenaar, Komdeur, & Richardson, 2008); red-cockaded woodpeckers (*Leuconotopicus borealis*; Daniels & Walters, 2000a); superb fairy-wrens (Cockburn et al., 2008); purple-crowned fairy-wrens (*Malurus coronatus*; Kingma, Hall, & Peters, 2013)). Here, inbreeding may be avoided through extra-pair mating with less related males (Cockburn et al., 2003; Kingma et al., 2013) and subsequently resolved since females that are mated with their son usually rapidly divorce to take up a vacancy elsewhere (Cockburn et al., 2003; Daniels & Walters, 2000b; Hidalgo Aranzamendi et al., 2016; Ribeiro et al., 2012; Walters, 1990). The latter suggests a potential role for maternal facilitation in territory inheritance, although an alternative explanation may be that

females in incestuous pairs disperse because males are dominant (Zahavi, 1990) either over unrelated males that aim to take the position with their mother (Hannon et al., 1985), or over their mother whom they may expel once they inherit the breeding position (note that the observation that fairy-wren females only divorce once a vacancy is available elsewhere suggests that females leave voluntarily once they have an alternative; Cockburn et al., 2003; Hidalgo Aranzamendi et al., 2016). More generally, asymmetry in competitive ability between males and females could partly explain why males are, on average, nearly twice as likely as females to inherit their natal territory (Table 2; *sensu* Emlen, 1995; see also figure 3 in Downing et al., 2018). Thus, in some species or circumstances, opportunities for territory inheritance may be restricted, and the factors that underlie such restrictions (e.g., relatedness to breeders, sex, queue length) need to be considered when aiming to determine the role of territory inheritance in explaining delayed dispersal (Kokko & Ekman, 2002).

Territory inheritance appears to be a common route to breeding (Table 2), but it is important to ask whether this route to breeding actively selects for delayed dispersal, or whether territory inheritance is an unselected consequence of individuals that delay dispersal for other reasons. Across species, the percentage of individuals who gain a breeding position through inheriting is only slightly lower than those gaining a position through shifting to an adjacent territory (Table 2). If territory inheritance occurs as a random consequence of philopatry, shifting should be a much more common route to breeding (as there are usually multiple adjacent territories, and just one natal territory). This suggests that, under certain circumstances (e.g., high breeder mortality, high density and competition, high relative competitive ability of individuals in the natal territory, or relatively good territory quality), the benefits of territory inheritance are probably sufficient to select for delayed dispersal. In line with this, Florida scrub-jays that inherit a breeding position have a higher life-time reproductive success than individuals that disperse and breed on non-natal territories (table 5.2. in Fitzpatrick & Bowman, 2016). This effect reportedly derives from increased mortality of dispersers in the few years post dispersal (leading to shorter average tenure duration), but it remains unclear whether local breeding *per se*, or for example intrinsic quality differences (e.g., in age or condition) between inheriting and dispersing individuals can explain the difference in life-time reproductive success. To what extent the expectation of territory inheritance can determine individual decisions to delay dispersal and whether delayed dispersal generally has evolved as a result of possibilities for territory

inheritance depends on several individual or species-specific circumstances (see Fig. 2 and Table 1), like group size or queue length (Kokko & Ekman, 2002; Williams & Rabenold, 2005), (variance in) territory quality (Dickinson, Ferree, Stern, Swift, & Zuckerberg, 2014), breeder mortality rates and relatedness among group members (Kokko & Johnstone, 1999; Lindström, 1986). Taken together, opportunities for future territory inheritance may well explain delayed dispersal by some species or individuals, either in isolation or, more plausibly (as predicted theoretically by Kokko & Ekman, 2002) in combination with other benefits of philopatry (Table 1) and supplementary options to obtain a breeding position that can be combined with staying in a natal territory. We will discuss those options below.

2.1.2 Territory budding via philopatry

Territory budding describes the process where philopatric individuals split off part of their natal territory, to subsequently establish a breeding position there (note that budding should not be confused with 'budding dispersal' referring to dispersal in groups; e.g., Gardner & West, 2006) (Fig. 1B). Budding has been described in only a few species and appears to be predominantly practiced by males (Table 2; but see Legge & Cockburn, 2000). While the general importance of budding among social species is unclear, it is the route to breeding taken by ca. 6% of male Seychelles warblers (Komdeur & Edelaar, 2001a), >10% of male purple-crowned fairy-wrens (Hidalgo Aranzamendi et al., 2016), >20% of male superb fairy wrens (*Malurus cyaneus*; Cockburn et al., 2003), >30% of laughing kookaburras (Legge & Cockburn, 2000), and 47% of male Florida scrub-jays (Woolfenden & Fitzpatrick, 1984). From what we know of it, the process of budding appears largely similar across species: the natal territory is expanded by fighting the neighboring group with help of the resident group members. Then, either before budding (Florida scrub-jay; Woolfenden & Fitzpatrick, 1978, 1984, 1990; Seychelles warbler; Komdeur & Edelaar, 2001a) or after budding (superb fairy-wrens; Cockburn et al., 2003; red-winged fairy-wren (*Malurus elegans*); Russell & Rowley, 2000) a subordinate male attracts an extra-group female with whom he then slowly expands the new territory (see figure 4 in Woolfenden & Fitzpatrick, 1978 and figure 2 in Komdeur & Edelaar, 2001a). Alternatively, budding can occur through only splitting off part of the natal territory, as occasionally occurs in purple-crowned fairy-wrens (by a natal male and an immigrant staging female; Hidalgo Aranzamendi et al., 2016; pers. obs.). Despite the

potential initial cost of conflicts with neighbors (Woolfenden & Fitzpatrick, 1990) and the risk of failing to permanently establish or further expand a relatively small territory (Fitzpatrick & Bowman, 2016; Legge & Cockburn, 2000; Woolfenden & Fitzpatrick, 1984), there appear to be several potential benefits of gaining a breeding position through this route. Komdeur and Edelaar (2001a) showed that budding subordinate Seychelles warblers had higher life-time reproductive success than those who floated or dispersed to breed in low- (but not high-) quality territories, partly because after breeding for a few years on their budded territory, these individuals could eventually also take over their natal territory or shift to an adjacent high-quality territory. Moreover, genetic and social familiarity is likely to make the border between the natal and newly-budded territories peaceful and low-maintenance (Bebbington et al., 2017; Dickinson et al., 2014; Fitzpatrick & Bowman, 2016; Gil & Stutchbury, 2010; Hatchwell, 2010; Legge & Cockburn, 2000). However, an individual's ability to capitalize on the potential benefits of budding depends on its ability to bud off part of the natal and/or adjacent territory. For example, individuals from high-quality territories and individuals of the more competitive sex are perhaps better able to expand and bud (Komdeur & Edelaar, 2001b). The most notable factor determining the success of budding, however, is probably the support of the breeders, who may tolerate or even facilitate it: in Florida scrub-jays, breeding males from the original territory can peacefully "intrude" into the newly established territory for years after the budding (Woolfenden & Fitzpatrick, 1990); in fairy-wrens, budding is tolerated by breeders (males only in superb fairy-wrens; Cockburn et al., 2003), and Seychelles warbler breeders and future budder expand the territory together before splitting off part of the territory (Komdeur & Edelaar, 2001b). Overall, the potential for budding may contribute to why some individuals remain philopatric for some time. However, the broader importance of budding remains to be determined, especially since budding events may go unnoticed if they are confused with birds shifting to a neighboring territory.

2.1.3 Shifting

We define shifting as philopatric individuals moving to a breeding vacancy in a directly adjacent territory (Fig. 1C). Across species, about one third of all individuals obtain their first breeding position by shifting (Table 2). Compared to budding, individuals that shift probably have fewer or no costs of establishing a territory, but the timing of moving is more opportunistic,

based on when a vacancy becomes available. Similar to those that bud or inherit, however, shifting individuals obtain benefits of philopatry while waiting for a vacancy to appear; do not have to engage in potentially costly movement through unfamiliar territories (see Section 2.2 and Table 1); may be supported by the breeders in the natal territory in competing for positions; and benefit from familiarity of the area and from familiar or related local individuals once in a breeding position (Zack, 1990; Zack & Stutchbury, 1992; see Section 2.1 and Table 1). Since it is plausible that philopatric individuals are quickly aware of neighboring vacancies, and territories are usually surrounded by multiple other territories, this route to breeding could be predicted to be more common than inheritance. However, as described above (Section 2.1.3), the percentage of individuals that obtains a breeding position by shifting is, on average, not much higher than the percentage that inherits a position. We suspect that this may be due to competition with other subordinates over breeding vacancies and/or because shifting has disadvantages. For example, shifting individuals may still end up pairing with related individuals (e.g., as is the case for 27% of females in superb fairy-wrens; Cockburn et al., 2003; see also Daniels & Walters, 2000a) because shifting is not generally sex-biased (Table 2) and genetic structure in social species often decreases over longer distances than just one territory (Hatchwell, 2010). Nonetheless, shifting is a common route to breeding (Table 2) and the potential opportunity to shift may be one important driver for delayed dispersal in social birds (Kokko & Ekman, 2002), especially given that the associated costs are limited and that the only prerequisites for individuals to shift is that they are initially tolerated in their natal territory and are able to successfully compete for the vacancy.

2.2 Independent breeding via extra-territorial movement

So far we have addressed the different routes to breeding that do not require extra-territorial movement. In many social species, however, a portion of the subordinate individuals leave their natal territory to roam through the population (Hunter, 1987). Some individuals "*prospect*" for breeding positions (or for other information; see below) and return to their natal territory if no suitable vacancy is found (Fig. 1D), whereas others permanently leave their natal territory to "*float*" through the population until they become independent breeders or die (see Moreno, 2016; Reed et al., 1999; Fig. 1E). Here, we synthesize what is known about extra-territorial movement and, by separating prospecting and floating, we highlight the

importance of distinguishing whether or not individuals can return to their natal territory to regain benefits of philopatry. For simplicity, we consider prospecting and floating as conceptually distinct here but distinguishing them in studies on wild birds may be difficult because individuals may return months after they left (e.g., hoatzins *Opisthocomus hoazin*; Strahl & Schmitz, 1990; see also below). Therefore, the costs and benefits of extra-territorial movement may rather be seen as a continuum based on how long subordinates spend away from their resident territory (Ridley et al., 2008).

Detailed empirical studies describing and/or quantifying prospecting and floating in social birds are rare (but see, e.g., Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020; Hooge, 1995; Kingma, Bebbington, Hammers, Richardson, & Komdeur, 2016; Kingma, Komdeur, Hammers, & Richardson, 2016; Langen, 1996a; Raihani et al., 2010; Ridley et al., 2008; Ridley, 2012). This is not surprising: it is difficult to follow individuals moving outside their territory as such movements may be irregular, rare and unpredictable and individuals often move rapidly and secretively through unknown environments (Arcese, 1987; Kingma, Bebbington, et al., 2016; Kingma, Komdeur, et al., 2016; Ridley et al., 2008). We can roughly estimate how many individuals engage in these behaviors given that individuals that obtain a territory other than their natal or directly adjacent territory must, by definition, have prospected or floated at least briefly. As floaters and prospectors may have died before obtaining a position, may have been unsuccessful and returned to their natal territory, or may have moved outside a study area (Kingma, Bebbington, et al., 2016; Koenig et al., 2000; Koenig, van Vuren, & Hooge, 1996), any estimate based only on dispersal data is by necessity an underrepresentation. Nonetheless, this minimum estimate of prospecting/floating is substantial (Table 2): 29% of males and 50% of females obtained a breeding position at least two territories away from their natal territory. There is, however, extensive variation among species: in some species individuals never or rarely move further than a neighboring territory, suggesting that prospecting or floating is very rare (e.g., Mexican jays *Aphelocoma wollweberi*, male Galápagos mockingbirds *Mimus parvulus*, splendid fairy-wrens *Malurus splendens*, and male superb fairy-wrens; Table 2), whereas in other species most individuals engage in extra-territorial movement before obtaining a breeding position (e.g., red-cockaded woodpeckers, acorn woodpeckers, white-browed sparrow-weavers *Plocepasser mahali*, groove-billed anis *Crotophaga sulcirostris*, western slaty antshrikes *Thamnophilus atrinucha*; Table 2). It is possible that these

interspecific differences arise through differences in costs and benefits of both delayed dispersal and extra-territorial movement. In this light, we outline the costs and benefits of prospecting (Section 2.2.1) and floating (Section 2.2.2) below after first briefly outlining some similarities that apply to extra-territorial movement in general.

General aspects of extra-territorial movement: Although extra-territorial movements may result in other benefits (like extra-group fertilizations; Langen, 1996a; Williams & Rabenold, 2005), they likely predominantly serve in the assessment of the environment and the current or future availability of breeding vacancies (Barve, Hagemeyer, et al., 2020; Kokko & Ekman, 2002; Pärt, Arlt, Doligez, Low, & Qvarnström, 2011; Reed et al., 1999; Woolfenden & Fitzpatrick, 1978). However, empirical demonstrations of this derive mainly from floaters in non-social species (Pärt & Doligez, 2003; Reed & Oring, 1992; Reed et al., 1999; see also Ponchon et al., 2012 and references cited therein), the benefits of extra-territorial movement in social species have received remarkably little empirical attention or support (Ekman et al., 2004), and it remains unclear how individuals detect vacancies. Therefore, whether extra-territorial movement results in a higher probability of finding and obtaining a position or a position of better quality than delayed dispersal (as assumed by theoretical models; e.g., Kokko & Ekman, 2002) remains to be tested in more detail, especially since local individuals may have a competitive advantage in filling a vacancy (see Zack & Rabenold, 1989 and Section 2.1). The costs of extra-territorial movement, on the other hand, have been invoked as a key explanatory factor in current theories of delayed dispersal. Emlen's (1982) extension of the ecological-constraints hypothesis incorporated the idea that such costs may be an important component explaining delayed dispersal; individuals that leave behind the safe-haven of their natal territory to prospect or float may suffer injuries or mortality due to attacks by conspecifics or predators (Cox & Cusick, 2018; Kingma, Komdeur, Burke, & Richardson, 2017; Woolfenden & Fitzpatrick, 1978). Additionally, dispersers may suffer from nutritional stress and reduced physical condition associated with movement through unfamiliar terrain (because of reduced foraging time, need for vigilance, or suboptimal habitat; Curry & Grant, 1990; Kingma, Bebbington, et al., 2016; Kingma, Komdeur, et al., 2016; Ridley et al., 2008; Ridley, 2012) which in turn may lead to disease, reduced competitive or reproductive ability, and mortality (Ridley et al., 2008). The extent of these costs likely depends on the duration individuals spent out of their territory (as shown by Ridley et al., 2008), whether or not individuals can join another

territory ("*staging*"; Section 2.3) and whether they can return to their natal territory ("*prospecting*"; Section 2.2.1).

Whether individuals disperse alone or in coalitions may also alter individuals' motivation or the outcome of extra-territorial movement. Both prospecting and floating may take place in coalitions: in several species (e.g., Arabian babblers, brown Jays, green woodhoopoes, Tasmanian native hens *Tribonyx mortierii*, chestnut-crowned babblers *Pomatostomus ruficeps*; Goldizen et al., 2002; Ligon & Ligon, 1990; Ridley, 2012; Rollins et al., 2012; Williams & Rabenold, 2005), small groups of often same-sex relatives (Ligon & Ligon, 1990; Williams & Rabenold, 2005; but see Sharp, Simeoni, & Hatchwell, 2008) come together to form coalitions for extra-territorial movement (e.g., on average 2.1 males or 3.5 females in Arabian babblers; Ridley, 2012; Zahavi, 1990). Dispersal in coalitions (also referred to as "*budding dispersal*"; Gardner & West, 2006; Rodrigues & Taylor, 2018) has been little studied in birds compared to mammals (e.g., Bradley, Doran-Sheeny, & Vigilant, 2007; Doolan & Macdonald, 1996; Maag, Cozzi, Clutton-Brock, & Ozgul, 2018), although more systematic work has been conducted on dispersal coalitions in birds since Cockburn's (1998) call to study such alliances (e.g., Barve, Lahey, et al., 2020; Heinsohn, Dunn, Legge, & Double, 2000; Ridley, 2012; Sharp et al., 2008; Williams & Rabenold, 2005). Coalitions may substantially alter the costs and benefits of dispersal (Koykka & Wild, 2015; Rodrigues & Taylor, 2018): most notably, individuals in coalitions can benefit from reduced per-capita vigilance (*sensu* Ridley et al., 2008) and improved protection, overall vigilance and safety-in-numbers (Cheney, 1983), resulting in reduced physiological (e.g., body mass loss and stress hormone levels) and mortality costs (Ridley, 2012; Young & Monfort, 2009). For example, Arabian babblers that disperse in coalitions lose less body mass in the 2 weeks following dispersal compared to solitary dispersing individuals (Ridley, 2012). Alternatively or additionally, individuals in coalitions may be better at competing for vacancies, even usurping existing breeders (e.g., Hannon et al., 1985; Lewis, 1982; Ridley, 2012), and they can derive kin-selection benefits when a related individual obtains a breeding position (Gardner & West, 2006; Lewis, 1982; Ligon & Ligon, 1990; Sharp et al., 2008; Williams & Rabenold, 2005). Thus, extra-territorial movement in coalitions may yield substantially increased direct or indirect fitness benefits (Heinsohn et al., 2000), and whether and how this promotes individuals to leave their natal territory remains a key topic for further study. In addition, in many species (like Florida scrub-jays, purple-crowned fairy-wrens and

Seychelles warblers; Woolfenden & Fitzpatrick, 1990; SAK personal observation) individuals do not disperse in coalitions despite similar potential benefits, raising the question of why coalition dispersal is common in some species (e.g., 42% of dispersal events in Arabian babblers; Ridley, 2012), but not in others.

2.2.1 Prospecting

In many social bird species, subordinate philopatric individuals undertake temporary extra-territorial prospecting trips (defined also as a *foray* or a *stay-and-foray* strategy; Brown, 1987; Kokko & Ekman, 2002) away from their natal territory (e.g., Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020; Kesler & Haig, 2007; Kesler, Walters, & Kappes, 2010; Kingma, Bebbington, et al., 2016; Kingma, Komdeur, et al., 2016; Reed et al., 1999; Raihani et al., 2010; Williams & Rabenold, 2005; Woolfenden & Fitzpatrick, 1984, 1990; see Fig. 1D). Prospectors may obtain important environmental and social information while prospecting (Reed et al., 1999), such as spatial variation in habitat quality (Koenig et al., 1992), performance of breeders (Cockburn et al., 2003) and availability of breeding vacancies (Kokko & Ekman, 2002). Theoretical work on dispersal has shown the importance of "informed dispersal" where individuals base dispersal decisions on previously acquired information (Bocedi, Heinonen, & Travis, 2012; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009; Delgado, Bartoń, Bonte, & Travis, 2014; Schmidt, Dall, & van Gils, 2010; Travis et al., 2012). Moreover, such visits can also function as advertisement to the receiving group or to create social familiarity. For example, in brown jays prospecting improves the likelihood that individuals will later be accepted in a (shorter) queue for a breeding position in a previously visited group, suggesting that prospecting individuals may not only obtain information about future breeding opportunities but also create social familiarity with the group or advertise suitability to the group (Williams & Rabenold, 2005). In social species where habitat saturation and limited breeder mortality constrain independent breeding, or where the quality of breeding positions is highly variable (Schjørring, 2002), information-gathering via prospecting could be particularly important. Thus, a greater understanding of prospecting is needed in social species because the factors driving this behavior may explain variation in delayed dispersal within and across species (Williams & Rabenold, 2005).

The few studies on the benefits of prospecting in social species suggest that, compared to fully philopatric individuals, prospectors can find a breeding vacancy faster and thus presumably have longer breeding tenure

(Kingma, Bebbington, et al., 2016; Woolfenden & Fitzpatrick, 1978; Zack & Stutchbury, 1992). As an additional benefit, when prospectors obtain a breeding position further away or sample a greater area, they may find a higher quality position (Koenig et al., 1992), experience reduced kin-competition, and/or obtain a less related partner compared to philopatric individuals who are restricted to obtaining a position at home or nearby (Table 1). Theoretical models assessing prospecting as a route to breeding assumed that these benefits are relatively small, as prospecting was assumed to only result in the acquisition of a breeding position relatively nearby due to a limited range of sampling. Although this is probably the case in species where prospecting trips are relatively brief or cover a relatively short distance (e.g., only 1.9 h in Micronesian kingfishers *Todiramphus cinnamominus* and <24 h to usually neighboring territories in brown jays; Kesler & Haig, 2007; Williams & Rabenold, 2005), in other species prospecting trips last much longer (one or more days in Florida scrub-jay females; Woolfenden & Fitzpatrick, 1990; see also Strahl & Schmitz, 1990) and cover greater distances (up to 12 territories in Seychelles warblers, and several kilometers in Florida scrub-jays, laughing kookaburras, red-cockaded woodpeckers and acorn woodpeckers; Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020; Hooge, 1995; Kesler et al., 2010; Kingma, Bebbington, et al., 2016; Kingma, Komdeur, et al., 2016; Koenig et al., 1996; Legge & Cockburn, 2000; Woolfenden & Fitzpatrick, 1984, 1990). Therefore, prospecting may be more effective in terms of finding a (high-quality) breeding position beyond the periphery of the natal territory than assumed (Kingma, Bebbington, et al., 2016).

Although prospecting may yield substantial benefits, the behavior seems generally quite rare (e.g., 4.3% of observations in Micronesian kingfishers (Kesler & Haig, 2007), 14% of individuals in Seychelles warblers (Kingma, Komdeur, et al., 2016), and 12–54% of subordinate female red-cockaded woodpeckers (Kesler et al., 2010)). While this is likely at least partly an artifact of the inherent difficulty in detecting prospectors, one reason why individuals do not prospect more may be that it is too costly (Bonte et al., 2012; Emlen, 1982; see Section 2.2 for an outline of these costs). Although the costs of prospecting (Table 3) (e.g., reduced body condition) are in most cases temporary and can be overcome when individuals return home (Kingma, Komdeur, et al., 2016), prospectors may trade off prospecting with genetic benefits of philopatry (i.e., indirect benefits of helping or own reproduction) as time- or energetic constraints associated with prospecting may inhibit helping and reproductive behavior

Table 3 The importance of having access to and/or being able to return to the natal territory is demonstrated by the lower survival costs associated with prospecting compared to floating (all costs relative to philopatry without prospecting behavior).

Species	Behavior	Effect relative to philopatry	References
Arabian babbler	Prospecting	4% reduced body mass[b]	Zahavi (1990) and Ridley (2012)
Seychelles warbler	Prospecting	5% reduced body mass; no survival effect	Kingma, Komdeur, et al. (2016)
Florida scrub-jay	Prospecting	Reduced survival[a]	Woolfenden and Fitzpatrick (1978) and Woolfenden and Fitzpatrick (1990)
Pied babbler	Floating	Continuous loss of body mass (up to 16%)[b]	Ridley et al. (2008)
Stripe-backed wren	Floating	Reduced survival[a]	Rabenold (1990) and Yaber and Rabenold (2002)
Hoatzin	Floating	Reduced survival[a]	Strahl and Schmitz (1990)
Seychelles warbler	Floating	Reduced survival	Kingma, Bebbington, et al. (2016)
Galápagos hawk	Floating	Reduced survival	Faaborg and Bednarz (1990)
Red-cockaded woodpecker	Floating	Reduced survival	Walters (1990) and Walters, Doerr, and Carter (1992)
Siberian jay	Floating	Reduced survival (predation)	Griesser et al. (2006)
White-throated magpie-jay	Floating[c]	No or slight survival cost[c]	Langen (1996a)

[a]Indirect evidence based on an association between sex-specific movement and sex-specific mortality (Florida scrub-jay and stripe-backed wrens), or evidence based on limited sample size (hoatzins).
[b]Survival costs not quantified
[c]Annual survival probability of white-throated magpie-jay floaters is 0.86 compared to 0.91 of non-breeders. Floaters in this species also differ somewhat from those in other species in that they often loosely associate with territorial individuals (Berg, Eadie, Langen, & Russell, 2009).

(Ridley, 2016; see also Young, Carlson, & Clutton-Brock, 2005, and Zöttl, Heg, Chervet, & Taborsky, 2013, for examples, in meerkats and cichlids respectively). Moreover, individuals may be punished by breeders if they refrain from helping before, during or after they prospect (Mulder & Langmore, 1993; see also Zöttl et al., 2013). Thus, although the physiological

costs of prospecting may be limited in the long term, benefits of not prospecting likely explain why individuals more often prefer to remain in a natal territory.

The decision to prospect is likely to be related to four key components that affect its cost (outlined in Fig. 2; see also, e.g., Pasinelli & Walters, 2002). First, intrinsic factors like sex, size, or body condition may determine individual ability to overcome the energetic costs of prospecting or to be competitive for a vacancy (Burkhalter, Fefferman, & Lockwood, 2015; Kingma et al., 2017; Pasinelli & Walters, 2002). For example, sex-differences in costs of prospecting (and floating) may explain sex-biased dispersal distances (Table 2; see also Kingma et al., 2017 for an example): females may prospect more and further away from their natal territory than males if they are less attacked by breeders in the territories that they intrude because they are considered less of a reproductive threat (male intruders may fertilize resident females whereas female intruders are unlikely to produce offspring in such territories). In line with this, dispersal in most avian cooperative breeders is female-biased. A notable exception is white-throated magpie-jays, which have male-biased dispersal: in this species, male intruders are not expelled when trying to obtain copulations with resident females and hence prospecting may not incur heavy costs for males (Langen, 1996b). Second, temporal and spatial variation in food availability may affect the ability of individuals to overcome the energetic costs of prospecting. Individuals may therefore be more likely to prospect in areas or times of high food abundance. The effect of environmental favorability or intrinsic condition on the decision to prospect might also be non-linear: whereas individuals in poor condition may not initiate extra-territorial movement, individuals from good quality territories may be more willing to stay. Thus, third, relative (dis)advantages of the natal territory or local area for future reproduction may determine context-dependent decisions to prospect (Fig. 3): for example, individuals may leave when their natal territory and local area is of poorer quality than other areas (see Komdeur, 1992; Pasinelli & Walters, 2002; but see Barve, Hagemeyer, et al., 2020), or when opportunities for obtaining a breeding position nearby are limited (e.g., when groups are larger (Barve, Hagemeyer, et al., 2020) and queues for inheritance are longer (Williams & Rabenold, 2005)). Fourth, since benefits of philopatry are important for delayed dispersal, individuals might prospect more when these benefits are fewer or smaller (e.g., limited nepotistic benefits, inability to reproduce as subordinate or reduced indirect fitness benefits). Thus, prospecting may be affected by a suite of factors (Fig. 2) and differences in these factors may ultimately explain the large variation in delayed dispersal and the

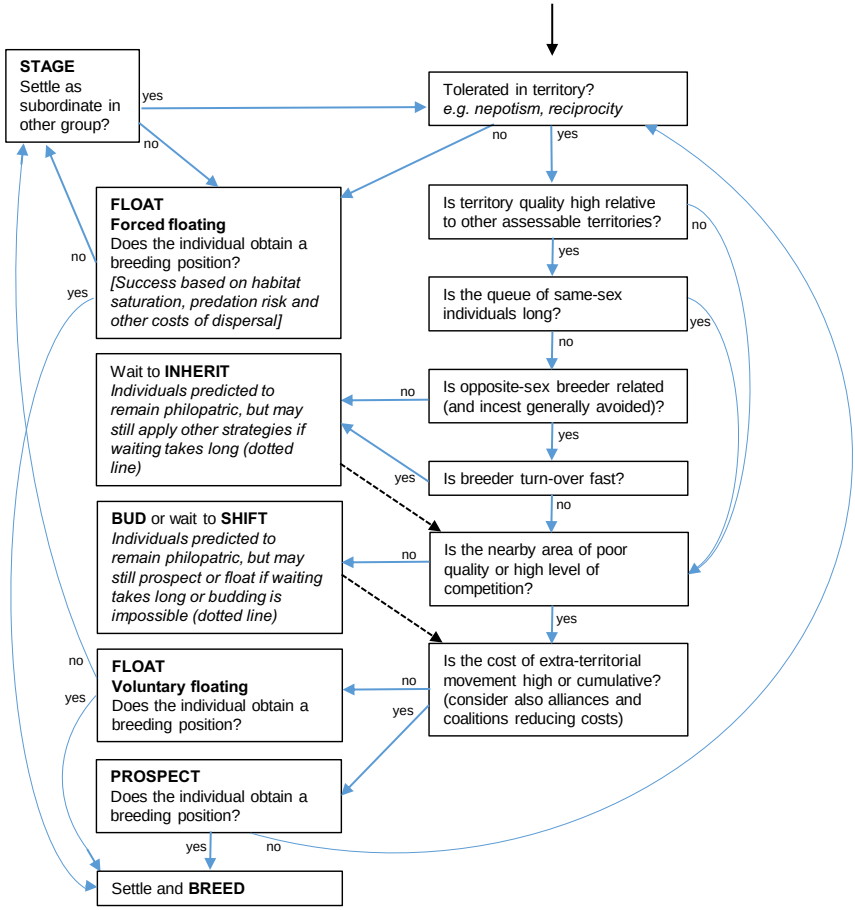

Fig. 3 A flowchart of under which social and environmental circumstances (boxes on the right) individual subordinates are predicted to follow certain routes to obtain an independent breeding position (left). Note that the effect of various proximate drivers underlying individual routes is probably not exhaustive (for example, individuals' body condition, quality and competitive ability may to some degree affect all the proposed routes to independent breeding; see also Fig. 2).

distance that individuals move to obtain a breeding position (see Table 3); comparative analyses might be an interesting way to test this.

Altogether, it is likely that the benefits of philopatry and costs of prospecting play a combined role in explaining delayed dispersal and the associated variation in dispersal distances. Future studies should therefore determine the costs and benefits of prospecting in terms of the acquisition of information about breeding positions and variance in quality of breeding

positions (as has recently been addressed in fish (Jungwirth et al., 2015) and mammals (Mares et al., 2014)). Interesting avenues to explore are, for example: (i) whether prospecting individuals can assess levels of competition and their own likelihood of success when competing over breeding vacancies (see Barve, Lahey, et al., 2020 as an exciting starting point); (ii) whether they can base decisions for local opportunities (e.g., to forego budding or to help raise young to augment the group) on prospects of breeding elsewhere; and (iii) whether they can estimate the productivity in a territory that may become available in the future (for example, based on reproductive output in such territories at the time of assessment; Cockburn et al., 2003; Zicus & Hennes, 1989). In order to assess the proximate factors driving prospecting behavior, recent advances in solar-powered radio-tracking appear extremely promising. For example, (Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020) established an automated radio-tracking system to track acorn woodpeckers. This system managed to capture the rate and distance of all prospecting events in remarkable detail and thus allowed the authors to assess in detail which individuals prospect, when, how long, and under what circumstances. We highly encourage the application of such a system in other species, as this will likely lead to important new insight in the process of informed dispersal and how individuals obtain a breeding position (Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020).

2.2.2 Floating

Individuals in several species roam or "*float*" though the population after permanently leaving their natal group (also referred to as a "*depart-and-search strategy*"; Brown, 1987; Kokko & Ekman, 2002; see Fig. 1E). While subordinate birds in a very small number of social species establish nomadic non-reproductive groups (e.g., consisting of 10–77 and 20–30 individuals in respectively Australian magpies *Gymnorhina tibicen* (Veltman, 1989) and American crows *Corvus brachyrhynchos* (Caffrey, 1992; see also Klomp & Furness, 1990)), floating usually involves single individuals or individuals in small coalitions (see above). Floating in social species resembles the route by which individuals in non-social species obtain a breeding position, although in social species the percentage of individuals that float is, by definition, much lower (e.g., 1–4% in Galápagos mockingbirds (Curry & Grant, 1990), 3% in pied babblers (Ridley et al., 2008), approximately 7% in red-cockaded woodpeckers (Walters, 1990), 5–10% in Arabian babblers (Zahavi, 1990), 16% in Tasmanian native hens (Goldizen et al., 2002), 16–18% in Seychelles warblers (Eikenaar et al., 2007), and 35% in Florida

scrub-jays (Woolfenden & Fitzpatrick, 1991); note, however, that these percentages are probably underestimates due to lack of detection and high mortality of floaters).

Like prospecting, floating might function in finding a vacancy faster and obtaining longer tenure, or in finding a breeding position of better quality (e.g., higher habitat quality, reduced kin-competition and/or less related partner; Table 1 and Fig. 2), but an important feature of theoretical models and conceptual studies of delayed dispersal is that floating is also associated with substantial costs (Kokko & Ekman, 2002; Walters et al., 2004). These costs mainly consist of permanently leaving all benefits of philopatry behind (see Table 1): floaters abandon opportunities to inherit the natal territory or shift to a neighboring one, access to food, protection, a share in reproduction in the group, and indirect fitness benefits from helping in the natal territory. Additionally, floaters may be expelled by territory owners to areas with limited food availability. Thus, floaters sacrifice substantial benefits and incur substantial costs, and it is often argued that this may explain delayed dispersal as a core prediction of the benefits-of-philopatry and ecological-constraints hypotheses.

Assuming that floaters leave voluntarily, have a high likelihood of detecting breeding vacancies and suffer a high cost, the behavior may reflect a high-risk high-gain strategy (see Kingma, Bebbington, et al., 2016). Like prospecting, however, the relative costs and benefits of floating (and thus the decision to adopt this strategy) probably depend on several proximate factors, taking effect when individuals are still in their natal territory or while they are floating (summarized in Fig. 2). For example, individuals may voluntarily decide to float when circumstances in the natal territory or local area are poor (e.g., large groups, poor territory quality, limited opportunities to breed). Such decisions may also be based on individuals' ability to compete for a vacancy (based on, e.g., sex, age or body size; Eikenaar et al., 2007; Zack & Rabenold, 1989; see also Van de Pol, Pen, Heg, & Weissing, 2007) and population characteristics that determine the relative benefits (e.g., availability of vacancies) and costs of floating (aggression of conspecifics, population density, predation risk). Therefore, individual condition and quality may well determine the onset and success of floating, but whether this is the case remains to be tested.

While so far we assumed floaters to leave voluntarily, in reality the lack of tolerance of group members in a natal territory (e.g., nepotism; Ekman & Griesser, 2002; Komdeur & Ekman, 2010; Nelson-Flower & Ridley, 2016) may be an important driver of floating (Fig. 3). Given that benefits

of philopatry can be substantial (see above), floaters are probably often expelled from their natal territory (Eikenaar et al., 2007; Groenewoud et al., 2018; Mulder, 1995). For example, after a turn-over of a breeder in the territory, the new territory owner may expel the unrelated subordinates that are present (Groenewoud et al., 2018; Kingma, Bebbington, et al., 2016). Not only breeders, but also (or only) higher-ranked siblings expel individuals from the territory in several species (gray jays *Perisoreus canadensis*; Strickland, 1991), red-cockaded woodpeckers (Hewett Ragheb & Walters, 2011), pied babblers (Ridley et al., 2008) and Siberian jays *Perisoreus infaustus* (Ekman, Eggers, & Griesser, 2002; Ekman & Griesser, 2016). Assessing whether floaters are expelled is important, because it might mean that they leave in suboptimal times with, for example, limited food availability. Moreover, ignoring the potential for eviction may obscure or artificially enhance the perceived influence of other factors, like territory quality, in driving dispersal decisions. Taken together, it becomes clear that it remains to be tested within and across bird species how various factors determine whether individuals decide or are forced to float and what the outcome of floating is; this constitutes an interesting and important step in order to gain a deeper understanding of delayed dispersal.

2.3 An intermediate step: Staging territories

In some species individuals leave their natal territory to join non-natal groups as a subordinate (referred to as "*staging*" or "*subordinate between-group dispersal*"; Cockburn et al., 2003; Groenewoud et al., 2018; see Fig. 1F). This occurs commonly in some species (for example, around 75% of individuals in brown jays, pied babblers, and (female) superb fairy-wrens; Cockburn et al., 2003; Ridley et al., 2008; Williams & Rabenold, 2005), and rarely or never in others (e.g., Tasmanian native hen, stripe-backed wrens; Goldizen et al., 2002; Piper et al., 1995; Yaber & Rabenold, 2002; see also species accounts in Stacey & Koenig, 1990). Since staging individuals do not immediately obtain a breeding position, they must move to a non-natal group for other benefits (comparable to some benefits of philopatry), or for opportunities for future territory acquisition. Comparing the situation in their natal territory with their new resident territory is a particularly tractable way to make inferences about the factors that promote individuals to stay as a subordinate in a group and to delay independent reproduction (Groenewoud et al., 2018; Nelson-Flower et al., 2018; Shen et al., 2017).

Motivations to settle in an unrelated group can be classified into two types, depending on whether individuals were forced to leave their natal

territory or whether they left voluntarily (Ekman et al., 1999, 2002). Firstly, the costs of extra-territorial movement of expelled subordinates may be reduced if they are accepted in the receiving group (e.g., Cockburn et al., 2003). For example, pied babbler floaters often join groups as subordinates because their condition is strongly reduced as a consequence of floating (Ridley et al., 2008). Second, individuals may settle in groups where they expect to acquire benefits, based on the quality of the area and a higher expectation of (future) breeding (Mulder, 1995). This may be driven by direct cues, such as queue length for inheritance (Nelson-Flower et al., 2018; Piper et al., 1995; Williams & Rabenold, 2005), opportunities for obtaining parentage (Baglione, Canestrari, Marcos, & Ekman, 2003; Groenewoud et al., 2018; Piper et al., 1995), habitat quality (Ekman et al., 2001), and/or indirect cues (like the number of formerly produced offspring; Cockburn et al., 2003).

While comparing the characteristics of territories where subordinates stage with the territory they left may provide extremely useful information about factors that determine individual decisions to leave (see Cockburn et al., 2003; Groenewoud et al., 2018; Williams & Rabenold, 2005), it is important to take into consideration why the receiving group would accept unrelated immigrants despite having to share territorial resources with the newcomer (as recently highlighted in a theoretical "dual benefits" framework; Koenig et al., 2016; Shen et al., 2017). For example, dispersal to groups with shorter breeding queues might seem adaptive on the part of the disperser because of a higher likelihood to inherit the territory (Nelson-Flower et al., 2018; Williams & Rabenold, 2005), but such a pattern could equally arise if dispersers are only accepted by small groups who benefit from group-augmentation effects like predation dilution (see Kingma et al., 2014; Ridley, 2016; Shen et al., 2017) or if smaller groups are unable to expel intruders (Lewis, 1982). Studies based on behavior and fitness of dispersers as well as territory owners are now needed to understand the dynamics and context of this process of settlement (or rejection) of staging individuals in a non-natal group (Kingma, 2018; Nelson-Flower et al., 2018).

Overall, staging may provide direct (reduced costs of floating, obtaining parentage) and/or future (chances to obtain a breeding position or obtaining a higher quality position) benefits, while some benefits of philopatry (e.g., nepotism, indirect fitness benefits) are sacrificed. Currently, however, we have limited understanding of what drives this behavior (Koenig et al., 2016). Therefore, an assessment of the prediction that staging is mainly applied by individuals (or species) that experience high costs of extra-territorial

movement, limited benefits of natal philopatry, and limited opportunities for independent reproduction would be worthwhile because this will ultimately help in explaining delayed dispersal in general (Groenewoud et al., 2018; Nelson-Flower et al., 2018; Shen et al., 2017).

3. Comparing routes to breeding: Costs and benefits across different fitness components

It is clear from our examples of how subordinates in different species obtain a breeding position (Table 2) that the importance of different routes to breeding strongly varies between species, and often also within species (e.g., between sexes or individuals of different quality, condition, status or age, and under different circumstances). The challenge remains to determine how this variation is explained by factors that determine the costs, benefits and constraints underlying these routes to breeding, which is the aim of this section. Different factors may play a role at different life stages: before (e.g., benefits of philopatry), during (likelihood of finding and obtaining a breeding position), or after (survival in a breeding position, or the quality of that position) an individual obtains a breeding position (Bowler & Benton, 2005; Fig. 2). Therefore, we deconstruct total fitness associated with each route based on four components (see Fig. 2 and Table 1): (i) subordinate reproductive fitness (own parentage) and indirect benefits of helping (Section 3.1); (ii) survival probability during searching or waiting for a breeding position (i.e., the costs of dispersal and survival benefits of philopatry; Section 3.2); (iii) duration of breeding tenure (Section 3.3); and (iv) reproductive quality as breeder (Section 3.4). For each of these components, we will discuss how its proximate drivers differ between different routes to breeding.

3.1 Subordinate fitness: Indirect benefits and own reproduction

Whether or not individuals decide to delay dispersal, stage or float may to some extent depend on whether they can obtain genetic benefits as a subordinate in their natal territory. This component of fitness may either be (i) indirect (kin-selected) if subordinates improve the survival or reproductive success of related individuals (Hamilton, 1964); or direct if subordinates obtain parentage (ii) in their territory or (iii) through extra-group matings (Cockburn, 1998; Hager & Jones, 2009). These opportunities may vary for different routes to breeding: indirect benefits are restricted to philopatric

individuals (and staging individuals if those settle with related individuals), local parentage may be available to philopatric and staged subordinates only, and extra-group parentage can, in principle, be obtained by all individuals regardless of whether they delay dispersal.

In many social species, individuals obtain indirect benefits in the natal territory from helping relatives (Griffin & West, 2003). Philopatric subordinates have the opportunity to help if their stay in the natal territory overlaps with breeders' subsequent breeding attempts, although prospectors may trade off the cost of extra-territorial movement with helping (as shown in mammals; Young et al., 2007). The prerequisites for indirect benefits are that helpers are related to the breeders, and that they can improve their reproduction or survival, as is the case in many species (see reviews in Cockburn, 1998; Griffin & West, 2003; Hatchwell, 1999; Kingma, Hall, Arriero, & Peters, 2010). Therefore it is not only important to determine relatedness between breeders and helpers, but also the circumstances under which helpers can improve reproductive success (e.g., in small groups or when temporal or spatial food availability is low; Stacey & Ligon, 1987). However, indirect benefits in the natal (or staging) territory generally do not exceed the reproductive benefits that an individual would obtain when breeding independently, at least in social birds (Clutton-Brock, 2002; Koenig & Mumme, 1987; Richardson et al., 2002; Stacey & Ligon, 1987). Moreover, indirect benefits of helping cannot explain delayed dispersal in group-living species that do not breed cooperatively, such as Siberian jays (Ekman et al., 1999; Griesser et al., 2017; Komdeur & Ekman, 2010). Nonetheless, in some cooperatively breeding species indirect benefits may tip the balance of costs and benefits of delayed dispersal versus floating (e.g., Koenig, Haydock, & Stanback, 1998), at least for some time.

Another potential genetic benefit of philopatry and staging is that subordinate females may co-breed (e.g., joint nesting; reviewed in Vehrencamp & Quinn, 2004) and subordinate males may fertilize eggs of females in their natal territory (Cockburn, 2004). Reproductive skew theory (reviewed in Hager & Jones, 2009) predicts that subordinate reproduction may be "allowed" by breeders as an incentive for subordinates to stay when they can substantially improve breeders' reproduction (e.g., when circumstances are harsh; Shen et al., 2012). While subordinate reproduction is found in some species (e.g., Barve, Hagemeyer, et al., 2020; Richardson et al., 2002; Shen et al., 2012), joint nesting is generally rare among birds, and in most species, reproducing male and female subordinates often only obtain a very small part of parentage compared to that obtained when breeding

independently (Cockburn, 1998, 2004; Downing et al., 2018; Vehrencamp & Quinn, 2004). Nonetheless, if during the same period individuals would float with limited opportunities to obtain parentage or a breeding position, the gain of some reproduction could partially explain why such individuals stay in a natal territory or a staging territory. This is supported by the patterns in "plural breeders" where multiple individuals can raise a brood in the same territory. Opportunities for raising their own brood is a strong incentive for subordinates to delay or forego dispersal (Brown & Brown, 1984): subordinates in species with plural breeding (see Table 2 for references) eventually breed in their natal territory substantially more often than individuals in species that have only one nest in their territory at the time (females: 38% ($n = 7$ species) vs 8% ($n = 21$ species); males: 48% vs 19%; Table 2), suggesting a reduced intention to disperse when individuals have opportunities to breed independently in their natal territory.

A third type of subordinate genetic benefits is that individuals could obtain parentage outside their group (Cockburn et al., 2008) either by extra-group fertilizations (males) or by intraspecific brood parasitism (females). Extra-group fertilizations could apply to both territorial subordinate males (either living in their territory, while prospecting or while staging), as well as floaters. However, in many cooperative breeders, extra-group paternity levels are rather low, and even in species with high levels of extra-group mating (like Seychelles warblers and superb fairy-wrens; e.g., Double & Cockburn, 2003; Richardson, Jury, Blaakmeer, Komdeur, & Burke, 2001) the proportion of subordinate males that obtains extra-group paternity is generally small (see Brouwer & Griffith, 2019, Cornwallis, West, Davis, & Griffin, 2010 for overviews). Extra-group copulations may be male-driven (e.g., in species where males court females or attempt forced copulations), but given that intruders are often chased by territory owners (Raihani et al., 2010), this seems unlikely to generally result in successful copulations (but see Langen, 1996a). Alternatively, extra-group mating can be female-driven, but it is unclear whether females target subordinates in such species, especially if these are floaters. For example, in the superb fairy-wren, females specifically target dominant and attractive males for extra-group copulations during brief directed pre-dawn visits (Double & Cockburn, 2000) and although resident subordinate males can occasionally obtain copulations with visiting females, the proportion that does so is rather low (Cockburn et al., 2009; Double & Cockburn, 2003). Nonetheless, the possibility that benefits of extra-group fertilizations are achieved via extra-territorial movement should not be discarded by

default: in brown jays, for example, prospecting males have been shown to sire offspring (Williams & Rabenold, 2005), and in some non-social species floaters obtain a portion of fertilizations (see table 2 in Moreno, 2016). Similarly, prospecting and floating females might potentially engage in intraspecific brood parasitism, by laying one or more eggs in the nest of non-natal groups. In line with intraspecific brood parasitism being rather rare in general in birds (MacWhirter, 1989; Yom-tov, 2008), there is only limited evidence that this occurs in social species. In white-fronted bee-eaters (*Merops bullockoides*; Emlen & Wrege, 1986) and moorhens (*Gallinula chloropus*; Gibbons, 1986) parasitizing females are usually breeders that were disrupted in their own breeding attempt or initiated an own brood after; it would be interesting to assess whether floating (or prospecting) could lead to specialized parasitism by females that have no option for independent breeding (see also Langen, 1996a). Taken together, however, the evidence suggests that extra-group parentage is unlikely to be a strong selective force behind either philopatry or floating, and it remains unclear whether philopatric or floating individuals would be more successful in obtaining such benefits. More systematic assessments across and within species, and explicit comparisons of such extra-group benefits between philopatric individuals and floaters, would be worthwhile to determine their relative importance for subordinate reproductive fitness.

Overall, in most species, subordinates are unlikely to obtain sufficient own parentage and indirect benefits to drive philopatry, staging, floating and delayed independent reproduction in isolation (although perhaps plural breeding species may be an exception). We suggest that other components must (also) be involved in explaining delayed dispersal and the intra- and interspecific differences in the applied routes to independent breeding.

3.2 Subordinate survival: Costs of extra-territorial movement vs survival benefits of philopatry

As part of the survival component of the benefits-of-philopatry hypothesis, many studies of delayed dispersal have focused on benefits in the natal territory like nepotism, reduced predation and higher food availability (reviewed in, e.g., Cockburn, 1998; Covas & Griesser, 2007; Ekman et al., 2001, 2004; Koenig et al., 1992, 2009, 2016; Shen et al., 2017; Walters, Copeyon, & Carter, 1992; Walters, Doerr, & Carter, 1992). The survival benefits of philopatry are very similar for philopatric individuals that eventually inherit, shift, or bud, and presumably quite similar for staging

individuals, and could explain why individuals do not float. Floaters leave all benefits of philopatry behind (Baglione, Canestrari, Marcos, & Ekman, 2006; Ekman et al., 2000; Griesser et al., 2006; Koenig et al., 1992; Zack, 1990; Table 1) and experience energetic and survival costs associated with extra-territorial movement (Bonte et al., 2012; Table 3). The costs of floating are probably more permanent and severe than those of prospecting or staging; a comparison of the costs of prospecting and floating (provided in Table 3) suggests that floating more often leads to reduced survival (in at least 6 of 7 species) than prospecting (1 of 3 species).

Whether the costs of floating and the benefits of philopatry (partly) drive delayed dispersal probably depends on a suite of determining factors (Fig. 2). First, predation risk outside a territory may limit the motivation for subordinates to leave a "safe-haven." This is determined by both predator density and the ability of individuals to float in coalitions to increase predator detection and dilute predation risk (Ridley, 2012). Conversely, living in a natal territory where predation risk is relatively high probably encourages individuals to leave. Second, individuals may be less likely to stage, prospect or float if natal food availability (determined by habitat quality and group size and composition; Dickinson et al., 2014; Ekman et al., 1999) is high (Baglione et al., 2006; Dickinson & McGowan, 2005; Komdeur, 1992; Stacey & Ligon, 1987, 1991; but see Barve, Hagemeyer, et al., 2020), or when there are large stretches of non-traversable areas (Brooker, Brooker, & Cale, 1999). While the prediction that individuals from good quality territories should delay dispersal is quite prominent, such individuals may also be in good condition and/or be good competitors, so that they may be more motivated to prospect or float. This contrast illustrates the difficulty of seemingly straightforward predictions, and highlights the importance of assessing whether and how individuals' condition affects the link between territory quality and prospecting and floating. Third, individuals may decide to prospect or float if their competitive ability while encountering conspecifics in other territories is high or the energetic costs of extra-territorial movement is relatively low. Therefore, size, sex, age, and other intrinsic factors that determine competitive ability, and whether individuals can float in coalitions, can all contribute to whether individuals move outside the territory (Fig. 2). Last, an important determinant for subordinates to stay is the acceptance of breeders (e.g., nepotism) and other subordinates (Nelson-Flower et al., 2018). While nepotism in itself is a well-established factor in explaining delayed dispersal (Ekman et al., 2004), we emphasize here that it is particularly important to empirically determine whether

individuals are forced or voluntarily leave a natal territory, as this can obscure the importance of other factors in explaining whether individuals stay or leave.

Many studies have recognized that combining the benefits of philopatry and the costs of floating are crucial in understanding delayed dispersal (Brown, 1987; Delgado et al., 2014; Ekman, 2006; Koenig et al., 1992; Kokko & Ekman, 2002; Russell, 2004). However, these costs and benefits only cover the survival component as subordinate. For example, the survival benefits of philopatry may have to be traded off against floating, which is riskier but may also yield a higher probability of obtaining a breeding position (see Kingma, Bebbington, et al., 2016). Therefore, unless individuals obtain sufficient direct or indirect reproductive fitness as subordinate (which appears to be rare; Section 3.1), the subordinate stage alone cannot fully explain selection on delayed dispersal because individuals ultimately require a breeding position to reproduce, which we outline in the next Sections 3.3 and 3.4.

3.3 Breeding tenure duration: Finding, obtaining and keeping a breeding position

A strong predictor of individuals' life-time reproductive success is how long individuals can hold a breeding position (referred to as "breeding tenure duration" in Fig. 2; see also, e.g., figure 1 in Ekman et al., 1999, and species accounts in Newton, 1989). Breeding tenure duration is the product of the age that individuals obtain a breeding position (determined by (i) the likelihood that they can fill a vacancy and (ii) they probability that they actually obtain the position), and (iii) the survival probability once they are a breeder (Fig. 2). Each of these three elements and the factors that determine them may differ strongly between individuals following different routes to breeding as we outline in turn below (see Fitzpatrick & Bowman, 2016 for an empirical example). Important to note is that the likelihood (or age) of finding and obtaining a position and the time spent as breeder may not only differ between floaters and philopatric individuals, but also between philopatric individuals following different routes to breeding (Table 1 and Fig. 2).

Breeding tenure duration can vary depending on the age at which individuals start breeding independently, which is partly determined by the likelihood that individuals find a vacancy. Indeed, the reduced probability of finding a vacancy in social compared to non-social species is the foundation of the ecological-constraints hypothesis (Emlen, 1982). Broadly, the probability of finding a vacancy is strongly determined by the availability of

vacancies, which in turn depends on local and population-wide breeder mortality rate and density (e.g., Curry & Grant, 1989; Pasinelli & Walters, 2002; Walters, Doerr, & Carter, 1992). Therefore, it can be predicted that if mortality rate of breeders is high compared to that of subordinates, philopatric individuals may have a high chance that a local vacancy becomes available in the near future, either in a natal ("*inheritance*") or nearby ("*shifting*") territory (Cant & English, 2006). On the other hand, if (local) breeder mortality is low, individuals may have to wait a long time and they may ultimately have to adopt other strategies to create a breeding position (budding) or find a vacancy (prospecting or floating; Bocedi et al., 2012). Whether floaters indeed have a higher likelihood of finding a breeding position (as predicted by theoretical models; Kokko & Ekman, 2002), and whether this is also the case compared to prospectors, is unclear. Floaters do, by definition, monitor larger areas than strictly philopatric individuals (Zack & Stutchbury, 1992), but may also face restrictions (e.g., many white-throated magpie-jay floaters "circulated among a circuit of a few territories rather than wandering more widely"; Berg et al., 2009; Langen, 1996a; see also Arcese, 1987; Smith, 1978; Stutchbury, 1991). Moreover, while limited breeder mortality may promote extra-territorial movement, conversely, floating may be too costly and can also be predicted to occur less if breeder mortality is very low and chances of finding a territory vacancy are small (Walters, Doerr, & Carter, 1992); i.e., there may be a non-linear relationship between breeder mortality and the relative benefit of floating. Overall, assessing the probability that philopatric (including prospectors) and floating individuals find a vacancy and the age at which they do so, and what factors determine the success of the applied route, is crucial for future empirical study of mechanisms underlying delayed dispersal.

The age at which individuals obtain a breeding position via any of the different routes to breeding also depends on whether an individual can successfully compete with others for a found vacancy, and whether they are accepted as breeder by resident individuals. In the case of territory inheritance, the probability of filling the vacancy may strongly depend on the relatedness to the opposite-sex breeder (Daniels & Walters, 2000a; Kingma et al., 2011; Nelson-Flower et al., 2012) and the length of the queue of older same-sex individuals in the territory (Kingma et al., 2011; Williams & Rabenold, 2005; see also Field & Cant, 2009; Kokko et al., 2001). The latter is suggested by studies that show stagers often join groups as subordinates in which the queue to inheritance is shorter (e.g., Nelson-Flower et al., 2018; Williams & Rabenold, 2005). Similarly, it has been

shown that if the density of subordinate individuals is high throughout the population (increasing potential competition for vacancies), individuals are better off staying at home (e.g., Hannon et al., 1985; Zahavi, 1989). However, subordinates can also use context-specific strategies, basing their dispersal decisions on their ability to outcompete subordinate conspecifics. Numerous factors can shape this context-dependence, including intrinsic properties (e.g., sex, size and age; Eikenaar, Richardson, Brouwer, & Komdeur, 2008; Zack & Rabenold, 1989), and social factors like the ability to move and compete in coalitions (Ridley, 2012; Williams & Rabenold, 2005) or the support from resident breeders in budding, inheriting or shifting strategies (see Section 2). In addition, a reduction in condition associated with floating may make floaters poor competitors for breeding vacancies (Ridley et al., 2008), selecting against such behavior. All these factors may therefore determine whether individuals remain philopatric, or leave and float. Future work could investigate how the probability that individuals find and obtain a position and age of first breeding depend on the route that individuals follow (*sensu* Komdeur & Edelaar, 2001a and Fitzpatrick & Bowman, 2016; see below), and how this in turn depends on factors like the level of competition (breeder mortality and presence of competitors) and the competitive ability of an individual.

Although the probability that individuals find and obtain a position may drive delayed dispersal and floating, their breeding success depends on how long individuals can survive and reproduce in that position. This likely depends on the availability of food and the abundance of predators in the obtained territory, and the intrinsic costs or permanent somatic damage incurred in obtaining the breeding territory (Fig. 2). Both factors may strongly differ between different routes to breeding and therefore affect whether individuals follow different routes. For example, if individuals live in or next to a high-quality territory (relatively high food availability and/or low predator abundance) they may have a stronger incentive to wait longer to inherit or shift to such a position (Pasinelli & Walters, 2002) or to bud off part of it, than to search for a position elsewhere. Conversely, if individuals live in poorer areas, they may prospect or float to obtain information about higher quality areas and eventually move there (either as a stager or as a breeder). Whether or not stagers, prospectors and floaters obtain higher quality breeding territories is unclear, but some evidence suggests that individuals from poor quality areas are more likely to disperse than individuals from high-quality areas (e.g., Komdeur, 1992; Stacey & Ligon, 1987). Delayed dispersal may also be favored if other routes result in reduced

breeder survival due to costs that individuals experienced during the period spent obtaining the position. Especially since extra-territorial movement may induce stress and loss of body mass (Table 3), this may result in accumulated somatic damage, which may in turn reduce the lifespan of individuals (Hausmann, Winkler, & Vleck, 2005), so long-term costs, although hard to detect, may partly explain the rarity of prospecting and floating (see above). Because breeding tenure depends on breeder survival, which may vary with the quality of the position and the intrinsic state of an individual when they become a breeder (Hawn et al., 2007; Mourocq et al., 2016), an interesting avenue for future research would be to determine whether breeding position qualities (habitat quality, social group characteristics, intrinsic state at the start of breeding and individual condition during tenure) vary according to the route to independent breeding.

Because breeding tenure duration is often linked with life-time reproductive success (Fitzpatrick & Bowman, 2016), it can intuitively be believed that a higher chance to find and obtain a breeding position earlier in life leads to a greater number of offspring produced. However, this may not be as straightforward as it seems. A younger age of first reproduction may actually be associated with lower reproductive success (e.g., due to higher costs of reproduction as shown in green woodhoopoes; Hawn et al., 2007), so that individuals may do better when they first remain philopatric for some time. Several studies have shown that, individuals that postpone breeding have a higher life-time reproductive success (e.g., Hawn et al., 2007; Komdeur, 1992; Walters, Doerr, & Carter, 1992). However, measures of life-time reproductive success (e.g., number of fledglings) may also be misleading as proxy for fitness (see Walters, Doerr, & Carter, 1992). While our aim is not to define how to measure fitness in natural populations (see, e.g., Brouwer, Cockburn, & Van de Pol, 2020; Danchin, González-Dávila, & Lebreton, 1995; Grafen, 2006; Orr, 2009; Stinchcombe, Kelley, & Conner, 2017), particularly important to mention in the context of delayed dispersal is that earlier-reproducing individuals may have a greater contribution to population growth (Coulson et al., 2006; Walters, Doerr, & Carter, 1992). The issues surrounding measuring fitness in wild populations can be partly resolved by assessment of the number of recruits or grand-offspring, but to quantify whether an individual who produces more offspring later in life (e.g., after a period of philopatry) is more successful than an individual that produces fewer offspring earlier in life (e.g., after floating early) requires a detailed calculation of the net reproductive contribution to the population. Studies using "de-lifing techniques" that take into account reproductive

timing and standardized genetic contribution to population growth (Coulson et al., 2006; Walters, Doerr, & Carter, 1992) will be extremely interesting, as cruder measures of fitness might lead to erroneous conclusions about selection on delayed dispersal.

3.4 Reproductive success of breeders: Quality of the breeding position

The fourth component of an individual's fitness is the frequency and productivity of reproductive attempts as breeders, which are determined by the reproductive quality of the breeding position. This is affected by the quality of the territory, the social group, and the breeding partner (Fig. 2).

Territory quality is an important determinant for reproductive success and therefore individuals should be selected to obtain a good quality territory. As such, individuals may remain philopatric to inherit, shift or bud if food availability is high or predator abundance low in their natal territory or adjacent territories (Brouwer & Cockburn, 2020; Ekman et al., 2002; Goldizen et al., 2002; Pasinelli & Walters, 2002; Zack, 1990; note, however, that budding initially leads to a small territory). In addition, obtaining a breeding position in or near to a natal territory may reduce competition because of kin-cooperation (Dickinson et al., 2014; Gil & Stutchbury, 2010; Hatchwell, 2009, 2010; Lambin et al., 2001; Legge & Cockburn, 2000) or reciprocal altruism between familiar individuals (Bebbington et al., 2017; Ridley et al., 2005). Moreover, knowledge about local predators, food and suitable nesting spots may improve reproductive output, at least initially; this is most beneficial for individuals who inherit their natal or staging territory and experienced previous breeding attempts in their territory. Another potential benefit of these local routes to breeding is the presence of young siblings or group members who can become an inheriting individual's future helpers if individuals breed cooperatively (Kingma et al., 2014; Kokko et al., 2001). Following similar logic, when there are few helpers present in their natal territory, individuals might prospect or float to find a larger group (as in stripe-backed wrens; Zack & Rabenold, 1989; Zack, 1990). Low food availability and strong kin-competition in the natal territory may also select for floating, which may not only be beneficial for the floater itself, but also leave more per-capita resources to facilitate reproduction by relatives who remained in the territory (Bowler & Benton, 2005; Fig. 3).

The quality of a breeding position also depends on the quality of, and compatibility with, the breeding partner. One obvious factor that can promote staging, prospecting or floating is the risk that philopatric individuals

obtain a closely related partner. This is commonly the case for territory inheritance, where subordinates frequently end up paired to a parent (Kingma et al., 2017), but may also be a risk for shifting individuals if limited dispersal distances and limited sex-bias in dispersal lead to kin clustering (Ridley & Sutherland, 2002; but see Kingma et al., 2017). In many species, subordinates are not accepted in a vacant breeding position in the natal territory if they are related to the remaining opposite-sex breeder (see Section 2.1.1), and potential to inherit in the near future cannot explain delayed dispersal in such cases. Moreover, even if closely related individuals breed, the negative effects of inbreeding or mechanisms of inbreeding avoidance (like extra-pair mating) may select against delayed dispersal (Nichols, 2017; Perrin & Goudet, 2001). In this light, staging may be a beneficial strategy to ensure a high likelihood to "inherit" a territory with an unrelated partner. Similarly, individuals may stage, prospect or float to find a high-quality partner, and future work should incorporate sexual selection into the framework of routes to breeding in order to explore this idea (see Moreno, 2016). On the other hand, in several non-social species, familiarity with a partner has been shown to be advantageous for breeding success (Black, 2001; Sánchez-Macouzet, Rodíguez, & Drummond, 2014), and the increased likelihood to obtain a familiar partner via inheritance, budding with an opposite-sex unrelated subordinate or shifting might promote individuals to wait for a local position or partner to become available. These arguments highlight the somewhat limited understanding of how the characteristics of an individual's future partner can affect dispersal decisions; as proposed also by Moreno (2016) for floaters in general, this aspect also requires further study specifically for philopatric individuals in social species.

Overall, whether individuals remain philopatric and wait for a local position or engage in extra-territorial movement may strongly depend on the expected reproductive benefits in the obtained territory. However, it is unclear what the relative benefits are for philopatric individuals to either inherit, bud or shift, and whether stagers and floaters generally obtain a better-quality partner or breeding position than prospectors or philopatric individuals. More empirical studies exploring the differences in breeding position quality following different routes to breeding are needed to unravel the importance of this component in explaining delayed dispersal.

3.5 Overall selection: Combining fitness components of routes to breeding

The ultimate selection on delayed dispersal vs floating is built up from the four components described above, spanning the costs and benefits while

waiting for a position, while aiming to obtain a position, and while occupying a position (Bowler & Benton, 2005). Individuals are expected to initiate extra-territorial movement, i.e., float or stage, if the expected fitness is higher than the fitness of each of the routes to breeding that require subordinates to remain in the natal territory. Although we, and many other studies, have addressed each of the components as conceptually separate entities, it is important to note that selection acts through these in concert. For example, empirically comparing fitness of individuals that breed in or close to their natal territory with that of floaters (or long-distance dispersers) requires inclusion of differential survival of individuals that wait or search for a vacancy (component 2 in Fig. 2): only including floaters that settled will underestimate the relative fitness benefits of inheritance or local dispersal. Similarly, even floating may lead to a higher probability of finding a breeding vacancy or to a better quality territory than delayed dispersal when only assessing inheritance and shifting, but if philopatric individuals can also create a territory by budding or prospect and obtain a high-quality territory, delayed dispersal may still be the best strategy. As such, studies and hypotheses exploring the effect of single factors in isolation (like nepotism, food availability, habitat saturation) may be informative, but also risk creating an incomplete picture of selection overall. We encourage future studies aimed to unravel the evolution of delayed dispersal, to take the entire suite of options that individuals have to obtain a breeding position into consideration (including the effect of various proximate factors and the ultimate costs and benefits; Figs. 2 and 3). Clearly, achieving the goal to create an all-encompassing overview is complex at best, but we think that conceptually separating the different components of different routes to an independent breeding position is a good starting point when aiming to understand delayed dispersal.

4. Future directions

In order to create a general understanding of what drives individuals to delay dispersal, the challenge is now to unravel what proximate factors affect the various fitness components associated with each different route to breeding. Here, we provide an overview of promising avenues for future empirical, comparative and theoretical study embedded within the framework presented in Fig. 2.

4.1 Assessing life-time reproductive benefits of different routes to breeding

An important way of making inferences about whether and how selection favors delayed dispersal is by comparing the life-time fitness of individuals that float with that of individuals that follow other routes to breeding. Relatively few such studies have been conducted (e.g., Ekman et al., 1999; Fitzpatrick & Bowman, 2016; Komdeur & Edelaar, 2001a; Stacey & Ligon, 1987, 1991; Walters, Doerr, & Carter, 1992). Therefore, we encourage researchers to determine fitness of the various different routes to independent breeding (following, e.g., Brouwer et al., 2020; Coulson et al., 2006; Walters, Doerr, & Carter, 1992; see Section 3.3) and to explicitly consider the factors that may affect the link between fitness and routes to breeding (ideally including also intrinsic differences between individuals). Hereby, it is important to not only distinguish the routes that allowed individuals to obtain a breeding position but also include individuals that died during the waiting or searching period. Recent advances as a result of automated radio-tracking (Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020) have shown this to be a particularly promising tool to distinguish individual strategies that can also be applied to, e.g., accurately quantify mortality. Moreover, studies of life-time reproductive success should also distinguish what components (direct and indirect reproductive and survival benefits of philopatry, breeding tenure, or the quality of a breeding position; Fig. 2) are responsible for differences in fitness of individuals adopting different routes to breeding, since this will be very informative in determining what factors promote delayed dispersal. We realize that assessing life-time reproductive success requires detailed long-term data, and that these are not available for every study. However, in the absence of such data, it would still be worthwhile to systematically assess a subset of one or more components of fitness in relation to which route to breeding individuals applied under different circumstances, while remaining cautious that the non-studied fitness components might be relatively important.

4.2 Determining proximate drivers of different routes to breeding

More information about the drivers of individual strategies is needed in order to understand why the importance of different routes to breeding, and the factors that underlie those, vary within and between species.

Most notably, detailed assessments of the costs and benefits of prospecting and floating are rare, and probably partly because of this, it remains unclear what factors determine whether individuals engage in such behavior and whether they leave voluntarily or are forced. For example, do prospecting and floating function in acquisition of information for future or immediate dispersal, and ultimately lead to a higher likelihood of obtaining a position? Do they lead to a better quality breeding position or partner? Future studies could resolve such questions by applying radio- or satellite transmitters (see Barve, Hagemeyer, et al., 2020; Barve, Lahey, et al., 2020; Ekman et al., 2002; Hooge, 1995; Kesler & Haig, 2007; Koenig et al., 1996; Maag et al., 2018) to determine when, where and why individuals prospect or float, whether and when they are successful in obtaining a breeding position, and to determine the costs of the behavior. Regarding the latter, molecular biomarkers of remaining lifespan and LRS, e.g., telomere length (Eastwood et al., 2019; Hausmann et al., 2005), enable exploration how early life or early costs of dispersal (prospecting and floating) determine individuals' future lifespan and duration of breeding tenure.

It is clear that the relative importance of the various factors in explaining delayed dispersal differs between species. Nonetheless, gaining greater insight into how various factors determine different routes to breeding is important (even if the ultimate fitness effects remain unclear). This can be done through either experimental, theoretical or comparative study. Since many factors can simultaneously affect individual decisions and their success, we are specifically in need of experimental approaches that can manipulate one or more of these factors within the context of a field study. Various studies have shown the value of this approach, for example by removing breeders and creating vacancies (e.g., Brouwer & Cockburn, 2020; Eikenaar, Komdeur, & Richardson, 2008; Eikenaar, Richardson, et al., 2008; Zack & Rabenold, 1989), altering the social environment (e.g., Cox, Cusick, & DuVal, 2019; see also Kingma & Székely, 2019), or changing food availability (e.g., Covas, Doutrelant, & du Plessis, 2004; Dickinson et al., 2014). We encourage similar experiments in other studies, and additional manipulations like for example increasing or decreasing individual condition by supplemental feeding or handicapping individuals. Theoretically assessing the broad consequences of these factors in general models may also be informative to reveal what factors underlie different routes to breeding, for example by adjusting species-specific parameters to create testable predictions (see, e.g., Kokko & Ekman, 2002). Finally, comparative analyses may assist in the identification of variation in life history, social organization or mating system traits that explain delayed dispersal

(Covas & Griesser, 2007). For example, it could be determined whether species-specific rates of inheritance, budding, shifting or staging are affected by the severity of the landscape (e.g., spatial variation in food availability), local competition (e.g., queue length and local density) and/or breeder mortality, to assess whether individuals are more or less likely to delay dispersal when opportunities to breed locally are of good quality or high in number. Overall, the four components outlined in Fig. 2 may be useful for guiding future experimental, theoretical or comparative work, since this framework allows researchers to consider how certain factors can affect multiple fitness components at the same time.

4.3 Comparing social and non-social species

Comparing social and non-social species is an interesting approach for making inferences about factors that may drive delayed dispersal (Brown, 1987); for example, individuals in some non-social species are also constrained in independent breeding by habitat saturation but do not remain philopatric (Komdeur & Ekman, 2010). Although we do not specifically address non-social species throughout this review, such comparisons have proven fruitful and informative (e.g., Arnold & Owens, 1998; Cornwallis et al., 2010; Hatchwell & Komdeur, 2000; Jetz & Rubenstein, 2011). Perhaps the framework from Fig. 2 can be used to expand these comparisons, by testing whether and how social and non-social species differ in either of the four fitness components and/or their associated factors. For example, concerning indirect benefits of philopatry, Cornwallis et al. (2010) showed that cooperative breeding is more common in species with lower extra-group paternity (see also Brouwer & Griffith, 2019; Dillard & Westneat, 2016), reflecting that indirect benefits for subordinates can bring about at least some benefits of delayed dispersal to helping individuals. Similarly, in non-social species, offspring may leave because they are expelled or because the costs of floating are relatively low. Alternatively, or additionally, individuals in non-social species may be more successful in finding and filling a vacancy (e.g., because of higher breeder mortality (Arnold & Owens, 1998) and/or limited competition for vacancies (determined by a recruitment-mortality ratio)), or breeding positions may differ in reproductive quality so that it pays for individuals to disperse and aim to obtain a high-quality position as early as possible. Thus, future studies comparing characteristics of social and non-social species focused on the abovementioned fitness components can greatly contribute to furthering our understanding of the evolution of delayed dispersal.

5. Conclusions

The evolution of sociality is one of the most persistent and intriguing questions in modern evolutionary and behavioral biology, and delayed dispersal is at the base of this extraordinary phenomenon. In this review, we have highlighted that delayed dispersal consists of much more than a simple comparison between philopatry and floating, and that the numerous different routes to breeding can impact fitness across the entire lifespan of social animals. We hope that the stepwise assessment based on the fitness component framework outlined in Fig. 2 will help guide general and species-specific studies in unraveling what factors determine the costs and benefits of delayed dispersal. Specifically, we hope that it might help future studies to elucidate the importance of considering the various behavioral strategies and routes to breeding applied by individuals or species; an exciting aspect of social evolution that we feel is somewhat underexposed, especially in empirical studies.

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