



## RESEARCH ARTICLE

# Individual dispersal delays in a cooperative breeder: Ecological constraints, the benefits of philopatry and the social queue for dominance

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**Abstract**

- Delayed dispersal is a key step in the evolution of familial animal societies and cooperative breeding. However, no consensus has been reached on the ecological and social circumstances driving delayed dispersal.
- Here, we test predictions from the ecological constraints and benefits of philopatry hypotheses as well as the recently proposed dual benefits hypothesis to better understand the evolution of group-living and cooperative breeding. Furthermore, we consider how individual social circumstances within groups affect dispersal decisions.
- We examine 11 years of life-history information on a wild population of cooperatively breeding southern pied babblers *Turdoides bicolor*. We investigate the effects of ecological conditions, natal-group membership and individual social context on male and female dispersal delays, disperser survival and acquisition of dominance.
- Female dispersal decisions are generally unconstrained by ecological or social circumstances. In contrast, males disperse in response to relaxed ecological constraints, decreases in nepotistic tolerance or when low social rank in the queue for dominance decreases their likelihood of gaining a dominant breeding position. Early dispersal by end-of-queue males often leads to a head-of-queue subordinate position in a non-natal group, thereby increasing access to dominant breeding positions. However, males and females remaining in natal groups gain benefits of philopatry via increased survival and, for head-of-queue males, very high likelihood of acquisition of a breeding position.
- Overall, predictions from the dual benefits hypothesis best describe these results, while some predictions from each of the ecological constraints and benefits of philopatry hypotheses were supported. The benefits of living and working together (collective action benefits) in large stable groups are of central importance in shaping dispersal delays in southern pied babbler societies. In addition, position in the subordinate social queue for dominance is the key in determining access to reproduction, particularly for males. This research highlights the importance of considering the costs and benefits of individual social circumstances in dispersal

decisions and illustrates how the dual benefits hypothesis offers new perspectives in understanding delayed dispersal.

#### KEY WORDS

benefits of philopatry, cooperative breeding, delayed dispersal, dual benefits, ecological constraints, family living, social queue, southern pied babbler

## 1 | INTRODUCTION

Dispersal from the natal territory is a significant life-history event for many animals, and the timing of dispersal can greatly affect individual fitness (Greenwood, 1980; Groenewoud et al., 2016). Delayed dispersal is common in many species, resulting in the formation of societies that range in complexity from parents and adult offspring associating sporadically, to family living, to cooperative breeders where non-breeding adults help raise the young produced by other group members (Andersson, 1984; Cockburn, 1998; Drobniak, Wagner, Mourocq, & Griesser, 2015). The evolution of delayed dispersal is currently viewed as an important step in the evolution of cooperation, but surprisingly, the social or ecological factors that drive dispersal delays in most species remain unresolved (Kingma, Bebbington, Hammers, Richardson, & Komdeur, 2016; Koenig, Dickinson, & Emlen, 2016). Furthermore, how individual social circumstances affect the fitness payoffs of dispersal decisions has rarely been investigated (Kingma et al., 2016; Pasinelli & Walters, 2002; Wong, 2010). Teasing apart the selective pressures that affect the costs and benefits of delayed dispersal is central to our understanding of how this crucial life-history event evolved.

Delayed dispersal is predicted to result from both (1) constraints on leaving the natal territory and (2) the benefits of remaining on the natal territory, which are not mutually exclusive and may vary between sexes (Emlen, 1982; Greenwood, 1980; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992; Koenig et al., 2016; Stacey & Ligon, 1991). Dispersal may be limited by “ecological constraints” consisting of: (1) risks inherent in dispersal or living alone (floating), (2) low availability of mates and/or territories and (3) low chance of independent breeding (Emlen, 1982; predictions 1A–1D, Table 1). Concurrent with these predictions, ecological constraints on dispersal in various species include harsh environments, high levels of predation risk, high cost of floating or a dearth of resources needed to breed independently (Groenewoud et al., 2016; Ridley, Raihani, & Nelson-Flower, 2008; Spinks, Jarvis, & Bennett, 2000). In addition to ecological constraints, the “benefits of philopatry” may also drive dispersal delays; these can be summed up as unique benefits found only on the natal territory which positively affect survival, current fitness and future fitness (Koenig et al., 1992; Stacey & Ligon, 1991; predictions 2A–2E, Table 1). Such benefits may include inheritance of a high-quality territory, increased familiarity with the natal territory or gains due to nepotistic preferences by relatives (Clutton-Brock & Lukas, 2012; Dickinson, Ferree, Stern, Swift, & Zuckerberg,

2014; Ekman, Eggers, Griesser, & Tegelström, 2001; Nelson-Flower & Ridley, 2016). In some species, including southern pied babblers, individuals can become subordinate in non-natal groups (Kutsukake & Clutton-Brock, 2008; Nelson-Flower et al., 2011; Yager & Rabenold, 2002). Although experiments may be needed to elucidate why certain individuals disperse to non-natal groups, it is possible to use observational data to explore the benefits of philopatry in such systems while controlling for the benefits of group-living; such comparisons are rare.

Many of the predictions of the ecological constraints and benefits of philopatry hypotheses were developed through observations of species inhabiting temporally variable, harsh environments or groups formed through philopatry (Cornwallis et al., 2017; Griesser, Drobniak, Nakagawa, & Botero, 2017; Lukas & Clutton-Brock, 2017). However, delayed dispersal is also observed in benign and stable environments, and some cooperatively breeding species form groups through processes other than philopatry (Koenig, 2017). In addition, neither hypothesis addresses the important effects of group size on the benefits of group-living and hence delayed dispersal. Recently, the “dual benefits” hypothesis was proposed to integrate the effects of ecological forces in benign and stable vs. harsh and/or variable environments into a single framework, as well as clarify the benefits available from group-living independent of natal philopatry (Shen, Emlen, Koenig, & Rubenstein, 2017); predictions 3A–4C, Table 1). The dual benefits hypothesis also expands predictions regarding group size and group genetic make-up using insider–outsider conflict theory to understand the interests of “insiders” (group members) and “outsiders” (potential joiners) (Shen et al., 2017). Dual benefits refer to “resource defence” (RD) and “collective action” (CA) benefits, which are not mutually exclusive (Koenig et al., 2016; Shen et al., 2017). RD benefits allow access to physical resources that are critical for breeding or survival. These benefits are predicted to be important for species in spatially heterogeneous but temporally stable environments; non-kin are predicted to be excluded from groups, leading to an optimal group size of two (Shen et al., 2017). Alternatively, CA benefits are created by group social coordination and are predicted to be more important in harsh or temporally variable environments. CA benefits are predicted to lead to greater productivity per capita (up to an optimal group size), with non-kin able to join groups smaller than the optimal size (Shen et al., 2017). Overall, the predictions of the dual benefits hypothesis involve acceptance of non-kin into groups and whether group size affects dispersal, as well as predictions similar to those of the ecological constraints hypothesis.

Individual social circumstances are also likely to affect dispersal decisions (predictions 5A–5F, Table 1), although have been somewhat overlooked empirically (but see Kingma et al., 2016; Pasinelli & Walters, 2002; Tibbetts, 2007; Wong, 2010). Individuals can vary in relatedness to individuals in their group and consequently in both their access to direct reproduction, and the potential for conflict with unrelated competitors (Kokko & Ekman, 2002; Ridley & Sutherland, 2002). Similarly, social queues for access to future dominant breeding roles will affect the benefit of remaining in the group, with head-of-queue individuals more likely to benefit from delayed dispersal than those further back in the queue, who incur costs due to kin competition (the offspring depreciation hypothesis; Ridley & Sutherland, 2002). Social queues for dominance have been investigated with respect to dispersal delays in several theoretical and some empirical studies (Ekman et al., 2001; Kokko & Ekman, 2002; Kokko & Johnstone, 1999; Kokko & Sutherland, 1998; Pen & Weissing, 2000; Ridley & Sutherland, 2002; van de Pol, Pen, Heg, & Weissing, 2007; Williams & Rabenold, 2005). However, individual variation in queue position and other social circumstances are rarely considered concurrently with ecological factors in empirical studies of dispersal delays.

Here, we examine hypotheses regarding delayed dispersal, generate predictions (Table 1), and test these using observations collected over 11 years from a ringed, habituated population of cooperatively breeding southern pied babblers *Turdoides bicolor*. In this bird species, groups are sedentary and comprise an unrelated dominant breeding pair with adult male and female subordinate helpers that are typically the offspring of one or both dominant individuals (Nelson-Flower et al., 2011). These helpers can breed in the natal group when unrelated opposite-sex potential partners are present, but rarely do so (Nelson-Flower et al., 2011). Babblers benefit from group-living: high predation risk has created an efficient group-based sentinel system, and floaters living alone fare badly compared with when living in groups (Ridley, Nelson-Flower, & Thompson, 2013; Ridley et al., 2008). Nearly all offspring delay dispersal; those dispersing at a younger age are more likely to become floaters or subordinates in non-natal groups, while those dispersing at older ages are more successful in gaining dominance and thus breeding positions, an effect seen particularly in males (Nelson-Flower & Ridley, 2016; Raihani, Nelson-Flower, Golabek, & Ridley, 2010). Optimal group size, based on survival of offspring from the nestling stage, appears to be 5–6 adults (Ridley, 2016; A.R. Ridley, unpublished data). Small groups (sized 4 adults or smaller) are more likely to accept unrelated subordinates than are larger groups (Ridley, 2016). Social queues for dominance likely exist in both sexes: vacant breeding positions are filled by the eldest subordinate if the remaining opposite-sex dominant is unrelated; otherwise, an immigrant takes the position (Nelson-Flower, Hockey, O’Ryan, & Ridley, 2012; Nelson-Flower et al., 2013).

To investigate why animals delay dispersal from their natal groups (leading to the evolution of familial societies), we first test how variation in a suite of ecological and social factors affect dispersal delays for males and females, testing predictions from both

the ecological constraints and dual benefits hypotheses. We then explore the benefits of philopatry through consideration of the survival and reproductive benefits derived from natal vs. non-natal group-living, accounting for differences in individual social circumstances.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

Data were collected from 2003 to 2014 from a habituated, colour-ringed population of 45 groups of southern pied babblers at the Kuruman River Reserve (26°58’S; 21°49’E) in the Kalahari Desert, South Africa (habituation details: Ridley & Raihani, 2007a). Dominance status within groups was determined using behavioural cues and, for females, vocalizations during inter-group conflicts (Golabek & Radford, 2013). The mean group size ( $\pm SE$ ) was  $4.4 \pm 0.1$  adults (range: 2–12 adults); group size varied over time, with groups monitored for three or more years exhibiting size differences of  $3.3 \pm 0.5$ . The population pedigree was used to assess relatedness between group members; the pedigree was generated from genotyping of nine highly variable microsatellite loci, parentage analyses and life-history data (Nelson-Flower et al., 2011).

After dispersal, individuals were considered to be group members after at least 10 days of feeding and roosting together. Dispersal was often over short distances and dispersed birds were commonly re-sighted on or near the study site (Nelson-Flower et al., 2012). When individuals vanished and were not re-sighted, longer distance dispersal could not be definitively distinguished from death, a difficulty faced by many dispersal studies (Koenig, Van Vuren, & Hooge, 1996). However, periodic censuses of surrounding groups were conducted to look for dispersers, and neither immigration into groups nor fine-scale genetic structure was sex-biased, implying no sex-bias in dispersal distance (Nelson-Flower et al., 2012). Unringed immigrants with adult plumage were assumed to be yearlings; those with juvenile plumage were assumed to be 6 months (Ridley, 2016). Some dispersal events were involuntary due to eviction (Ridley, 2016). Eviction by subordinates of other subordinates was rare ( $N = 8$  evictions over 11 years) but preceded by protracted periods of overt aggression. Evictions occurred between individuals residing with their parents in natal groups, usually young males ( $N = 7/8$ , mean age of males  $243.6 \pm 27.9$  days old; the female evictor and evictee were sisters, both 634 days old). Half of these ( $N = 4$  males) resulted in immediate and permanent departures (two became floaters, two became non-natal subordinates), while the others returned to their groups 1–3 days later.

### 2.2 | Statistical analysis

Statistical analyses were performed within R v.3.4.0 (R Core Team, 2017). All statistical tests were two-tailed. For GLMMs, we used R packages “lme4” v.1.1.13 (Bates, Machler, Bolker,

& Walker, 2015) or “glmmadmb” v.0.8.3.3 (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2014) to specify GLMMs with binomial or negative binomial error structures. We examined survival probabilities using Program Mark (White & Burnham, 1999) and the R packages “RMark” v.2.2.2 and “coxme” v.2.2-5 (Laake, 2013; Therneau, 2015). We assessed model fit using Akaike’s Information Criterion adjusted for small sample sizes ( $AIC_c$ ; Burnham & Anderson, 2002). For analyses using GLMMs and Cox mixed effects models, models within 2  $AIC_c$  units of the best model were averaged using “MuMIn” v.1.15.6 (Bartoń, 2016), after excluding “nested” models (models that were more complex versions of the top model) from the 2  $\Delta AIC_c$  model set (Arnold, 2010). Tables are presented showing the resultant models in the 2  $\Delta AIC_c$  model set, and the full and null models; if averaging was employed, model estimates and SEs were calculated from full models as suggested by (Arnold, 2010). All continuous explanatory variables were centred and scaled to facilitate model comparisons; categorical variables involved in interactions were also centred for model comparisons and averaging (Grueber, Nakagawa, Laws, & Jamieson, 2011; Schielzeth, 2010). Means and SEs presented in figures were generated from minimal models identified through  $AIC_c$  comparison or through multi-model averaging (reviewed in Grueber et al., 2011). Figures were drawn with R package “ggplot2” v.2.2.1 (Wickham, 2009); figures of Cox model results were drawn using R package “survminer” v.0.4.0 (Kassambara & Kosinski, 2017).

### 2.3 | Ecological constraints and social contexts: Dispersal rates

We examined how ecological and social circumstances affected male and female dispersal per season, testing predictions 1B/3A, 1C, 1D/4A, 3C, 4C, 5A, 5B and 5C of Table 1. We divided each year into three seasons: the early breeding season (1 September–31 December), typified by low rainfall and a first breeding attempt; the late breeding season (1 January–30 April), typified by high rainfall and further breeding attempts; and winter (1 May–31 August), generally dry and cold with no breeding activity (Ridley, 2016). For each season, we examined the likelihood of dispersal from the natal group for male or female subordinates using mixed effects Cox models. Only those subordinates that were seen alive after departing the group and were 6 months old or older were included; males and females were analysed separately. Explanatory variables included: number of same-sex breeding vacancies in the population, rainfall (mm, a proxy for food availability, see Wiley & Ridley, 2016), mean distance to nearest neighbour (km, a proxy for available territory, hereafter “inter-group distance”), mean group size, a quadratic term for mean group size (previous work found an optimal group size for offspring survival Ridley, 2016), season (early breeding, late breeding or winter) and position in social queue (head or end). The genetic relationship with the dominant male affects male but not female dispersal

delays (relationships with dominant females do not affect delays) (Nelson-Flower & Ridley, 2016); therefore, in male analyses, we also included relationship with dominant male. Individuals were classified as the “head” of the social queue for dominance if they were the eldest subordinate of their sex, and as the “end” of the queue if there was a same-age (brood-mate) or older, same-sex subordinate present. We did not include multiple ranks indicating position in the queue because there were insufficient replicates of each rank for analysis. In cases where the eldest same-age subordinates were brood-mates, they were each conservatively classified as end-of-queue ( $N = 22/342$  female seasons,  $N = 20/200$  male seasons). Group identity and unique season identity nested within year were included as random terms, and the sample included each individual known to be alive after dispersal from its natal group (105 known-age subordinates at 20 groups). See Electronic Supplementary Material for details of calculations of rainfall, distance, same-sex breeding vacancies and specification of co-linear terms.

### 2.4 | Benefits of philopatry and queue position

We next explored the benefits of philopatry in different social contexts. First, we asked how natal group membership and queue position (“life-history stage”) affect survival according to sex and age (predictions 2A and 5D, Table 1). We were unable to distinguish long-distance dispersers from those that died, but accepting this constraint, multi-state survival analysis remains a useful window into the payoffs from different life-history stages. We estimated the probability of survival in MARK v. 8.2 via Rmark v. 2.2.2 (Laake, 2013; White & Burnham, 1999). At 6-month intervals from the age of 6 months old until 3.5 years old (the age at which 97.5% subordinates had gained dominance or disappeared), we determined an individual’s life-history stage: (1) head-of-queue in the natal group, (2) end-of-queue in the natal group, (3) head-of-queue in a non-natal group, (4) dominant or (5) vanished. The dataset included 226 known-age subordinates ( $N = 100$  males, 126 females) with known life histories. Because only one known-age female was end-of-queue in a non-natal group, we excluded this female (no males were end-of-queue in non-natal groups; see below).

Second, we investigated if natal and non-natal subordinates differed in their current direct reproductive and indirect (through helping) fitness benefits (predictions 2B and 2C, Table 1). We investigated whether adult subordinates were more likely to successfully breed in natal vs. non-natal groups, examining all subordinates, then only those living with an unrelated potential breeding partner. We included whether the subordinate ever bred or not as the response variable and group type, subordinate sex and their interaction as the explanatory terms in binomial GLMMs with group identity as random terms. We also investigated the indirect benefits available through helping at the time of dispersal by comparing subordinate relatedness to group offspring in natal and non-natal groups.

Third, we examined likelihood of acquisition of dominance (representing future direct fitness Nelson-Flower et al., 2011)

in relation to natal group membership and queue position (prediction 2D, Table 1). Immigrant subordinate females often joined groups containing other subordinate females; where their age was unknown (individuals from outside the study population), they were classified as end-of-queue (due to their assumed minimum age of 1 year old) ( $N = 96$  females; 16 were unknown age; seven were classified end-of-queue). Known-age females sometimes joined non-natal groups as end-of-queue subordinates (one incidence). Analyses that included females of unknown age were repeated after their exclusion (see Section 3). Males were never end-of-queue in non-natal groups; we therefore examined dominance acquisition first for head-of-queue males and females, and second for head- and end-of-queue females. For each analysis, whether or not subordinates were observed to ever acquire dominance was the response variable in a binomial GLMM. For the head-of-queue analysis, natal group, sex and their interaction were included as explanatory variables. The dataset included 108 observations (60 females and 48 males) of 95 known-fate head-of-queue subordinates in 34 groups. For the female analysis, natal group, queue position and their interaction were included as explanatory variables. The dataset included 96 observations of 83 known-fate female subordinates in 28 groups; after exclusion

of unknown-age females, the dataset included 80 observations of 68 known-fate female subordinates in 25 groups. Both analyses included group and subordinate identities as random terms.

Fourth, we explored whether residence in the natal group affected the age at which subordinates acquired dominance (prediction 2E, Table 1). Length of dominance tenure is likely to be a key predictor of lifetime reproductive success (Hodge, Manica, Flower, & Clutton-Brock, 2008). Subordinate age (days) at acquisition of dominance was the response variable in a GLMM with a negative binomial distribution (only subordinates that were seen to inherit or disperse to acquire dominance were included). Explanatory variables included the subordinate's sex, whether the subordinate lived in the natal group up to the point it acquired dominance, and the interaction. The dataset included 64 subordinates of known age and fate at 20 groups.

### 3 | RESULTS

#### 3.1 | Ecological constraints and social contexts: Dispersal rates

Subordinate females were more likely to disperse from natal groups when group size was small (estimate  $\pm$  SE; 95% confidence interval:

**TABLE 1** Theory and predictions regarding why animals delay dispersal from their natal group

Theory	Principle	Prediction in southern pied babblers
Ecological constraints (Emlen, 1982)	Dispersal is risky Mates or territories are not available Independent breeding is unlikely to succeed	1A Floating is costly 1B Increase in territory availability prompts dispersal (same as 3A) 1C Non-drought conditions prompt dispersal 1D Availability of breeding vacancies in stable groups prompts dispersal (same as 4A)
Benefits of philopatry (Koenig et al., 1992)	Survival improved Current reproductive success is improved  Future reproductive success is improved	2A Survival higher in natal groups than in non-natal groups 2B Direct (through breeding as a subordinate): higher in natal groups than in natal groups 2C Indirect (through helping raise kin): higher in natal groups than in non-natal groups 2D Acquisition of breeding position: more likely from a natal group than from a non-natal group 2E Age at acquisition: younger from a natal group than from a non-natal group
Dual benefits: resource defence (Shen et al., 2017)	Control of resources drives group-living Optimal group size is a pair	3A Increase in territory availability prompts dispersal (same as 1B) 3B Only kin accepted as subordinates 3C Group size does not affect dispersal or immigration attempts
Dual benefits: collective action (Shen et al., 2017)	Benefits gained by social coordination drive group-living Optimal group size is greater than pair	4A Dispersal in response to available vacancies in groups (same as 1D)  4B Non-kin accepted as subordinates until optimal group size is reached 4C In larger groups, dispersal is decreased and immigration attempts increase
Social context	Genetic relationship to opposite-sex dominant Genetic relationship to same-sex dominant Position in social queue for dominance	5A Presence of a potential breeding partner delays dispersal 5B Unrelated dominant males hasten subordinate male dispersal <sup>a</sup>  5C Queue position affects dispersal delay 5D Survival higher at head-of-queue 5E Reproduction more likely from head-of-queue 5F Dominance more likely from head-of-queue

<sup>a</sup>Prediction generated from results of Nelson-Flower & Ridley (2016).

$-0.788 \pm 0.316$ ;  $-1.408$  to  $-0.168$ ,  $p = .013$ , Figure 1, Table S1). Female dispersal probability was not affected by season, availability of breeding vacancies, inter-group distance (a proxy for available territory), rainfall or position in the social queue for dominance (Table S1). Subordinate males were more likely to disperse from natal groups when there were more breeding vacancies (estimate  $\pm$  SE:  $0.657 \pm 0.277$ ,  $p = .018$ , Figure 2a,b, Table S1), when rainfall was higher ( $1.401 \pm 0.433$ ,  $p = .001$ , Figure 2c,d, Table S1), when inter-group distances were smaller ( $-1.010 \pm 0.402$ ,  $p = .012$ , Figure 2e,f, Table S1), when they were end-of-queue ( $2.060 \pm 0.595$ ,  $p < .001$ , Figure 3a-c, Table S2), or when they were unrelated to the dominant male ( $1.389 \pm 0.550$ ,  $p = .012$ , Figure 3d-f, Table S2). Subordinate male dispersal probability was not affected by season or group size (Table S2).

### 3.2 | Benefits of philopatry and queue position

Survival probability was highest for dominants and head-of-queue natal subordinates, lower for end-of-queue natal subordinates and lowest for head-of-queue non-natal subordinates (Figure 4, Table S3). Membership in the natal group did not affect subordinate reproduction when considering all subordinates ( $-0.874 \pm 0.831$ ,  $p = .293$ ; Table S4a) or only those subordinates with potential breeding partners in their groups ( $0.343 \pm 0.947$ ,  $p = .717$ ; Table S4b). However, at the time of dispersal, subordinates were more related to the offspring produced by the dominant pair in natal groups ( $r = .387 \pm .015$ ) than in non-natal groups ( $r = .094 \pm .025$ ) (Wilcoxon signed-rank test,  $W = 1810.5$ ,  $p < .001$ ).

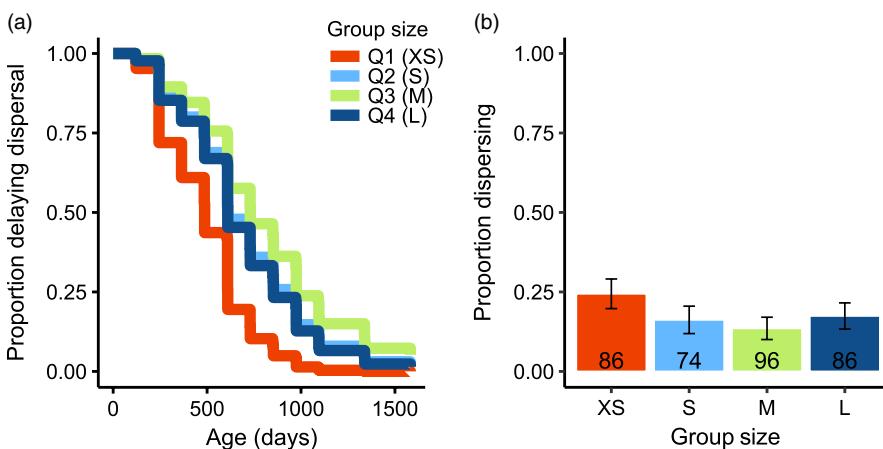
Females were equally likely to be head-of-queue in natal and non-natal groups (natal groups:  $N = 45/75$  (60.0%), non-natal groups:  $N = 15/21$  (71.4%); proportion test,  $\chi^2 = 0.492$ ,  $df = 1$ ,  $p = .483$ ). This result was unchanged after exclusion of unknown-age females (natal groups:  $N = 41/68$  (60.3%), non-natal groups:  $N = 10/12$  (83.3%); proportion test,  $\chi^2 = 1.452$ ,  $df = 1$ ,  $p = .228$ ). Males were far more likely to be head-of-queue in non-natal groups than in natal groups (natal groups:  $N = 25/54$  (46.3%), non-natal groups:  $N = 23/23$  (100.0%); proportion test,  $\chi^2 = 17.593$ ,  $df = 1$ ,  $p < .001$ ). In natal groups, male and female known-age, known-fate subordinates differed statistically in the proportion that were head-of-queue at 6 months old ( $N = 8$  males, 16 females), that were end-of-queue but

waited to become head-of-queue ( $N = 9$  males, 23 females), and that dispersed while end-of-queue ( $N = 27$  males, 22 females;  $\chi^2 = 6.726$ ,  $df = 2$ ,  $p = .035$ ).

End-of-queue males were never observed to acquire dominance through dispersal or inheritance, and males were only end-of-queue in natal groups. When considering head-of-queue males and females in natal and non-natal groups, we found that males in non-natal groups were significantly less likely to acquire dominance than those in natal groups (estimate  $\pm$  SE,  $-3.394 \pm 1.062$ ,  $p = .001$ ), hence philopatry conferred a significant benefit to males. No such benefit of philopatry was seen for head-of-queue females ( $-0.090 \pm 0.598$ ,  $p = .881$ , Figure 5a, Table S5a). When considering all females, only queue position affected female acquisition of dominance, with end-of-queue females less likely to become dominant ( $-0.929 \pm 0.464$ ,  $p = .045$ , Figure 5b, Table S5b). This effect remained when we excluded females of unknown age from the analysis ( $-1.075 \pm 0.491$ ,  $p = .029$ , Table S5c). Queue position did not appear to influence the likelihood of current reproduction in groups, but this was possibly due to small sample size resulting from high reproductive skew (all subordinates:  $N = 6/105$  head-of-queue bred,  $N = 1/65$  end-of-queue bred,  $\chi^2 = 0.784$ ,  $df = 1$ ,  $p = .376$ ; known-age subordinates only:  $N = 5/90$  head-of-queue bred,  $N = 0/59$  end-of-queue bred,  $\chi^2 = 1.753$ ,  $df = 1$ ,  $p = .186$ ). Age at which dominance was attained was unaffected by residence in a natal vs. non-natal group for males and females (estimate, 95% CI: Table S6).

## 4 | DISCUSSION

In southern pied babblers, dispersal is affected by a range of ecological and social factors that vary between the sexes. Female dispersal is driven by benefits associated with group productivity and females delay leaving larger natal groups. Male dispersal is driven by costs associated with searching for breeding vacancies, as well as social circumstances. Males disperse when rain (and thus food Wiley & Ridley, 2016) is plentiful, when inter-group distances are small or breeding positions are vacant, all of which are likely to decrease search costs for breeding vacancies. Males also disperse as a result of social conflict (with an unrelated dominant male; Nelson-Flower

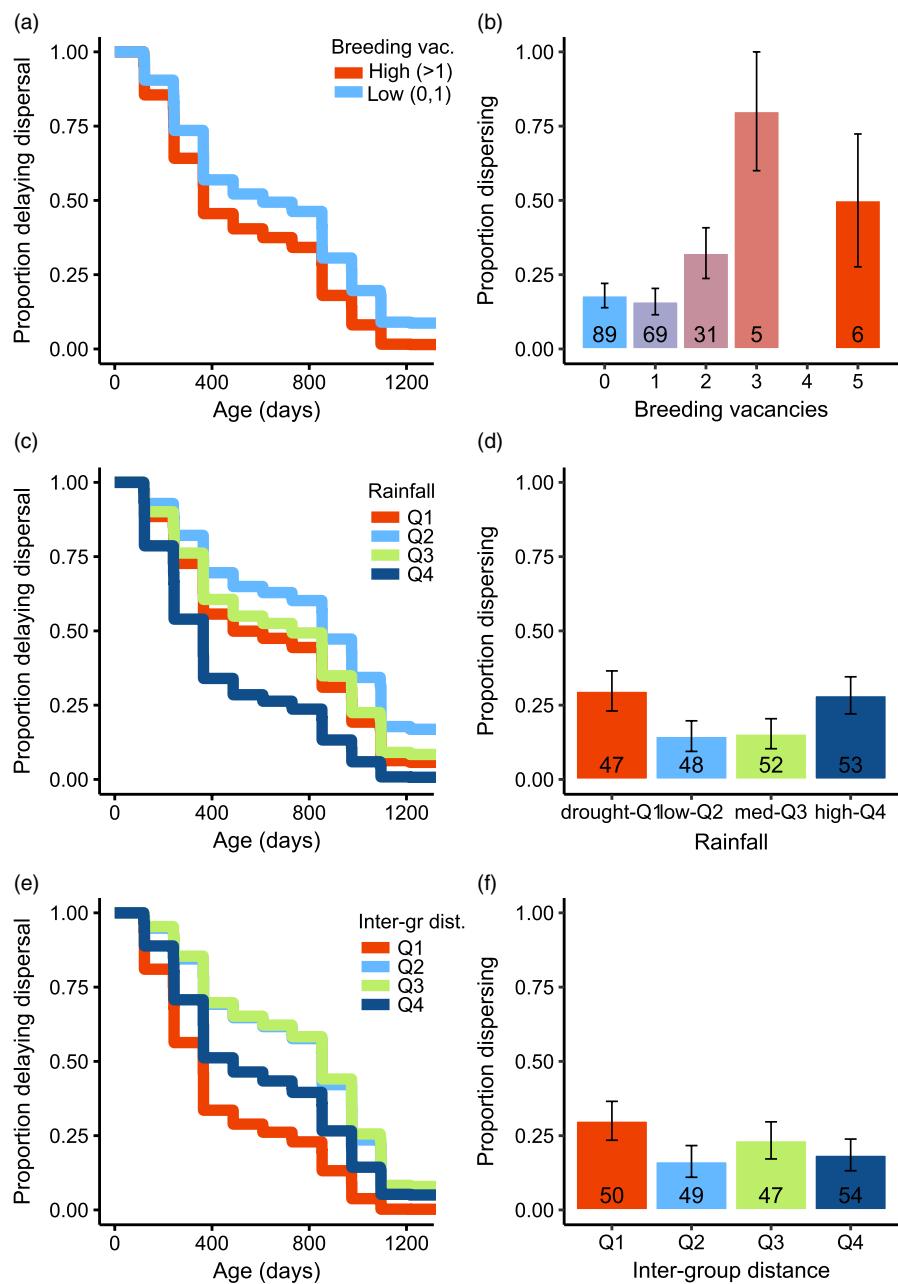


**FIGURE 1** (a) Female dispersal delay probability per season per group size quantile; (b) raw data of proportion ( $\pm$ SEM) of females dispersing per group size quantile. Numbers indicate sample sizes. Group size is categorized here for illustrative purposes and was a continuous variable in our analyses

& Ridley, 2016) or to improve social status. End-of-queue subordinate males invariably become head-of-queue subordinates if they disperse to a non-natal group. Head-of-queue position improves the likelihood of attaining a dominant breeding position for both males and females, and is particularly important for males, because end-of-queue males are never observed to gain dominance. However, survival is lower in non-natal groups and floating is costly (Ridley et al., 2008). Furthermore, males that are head-of-queue in natal groups are more likely to gain breeding positions than those in non-natal groups. Nevertheless, early dispersal appears to be an alternative mating tactic for end-of-queue males. Although females also benefit from being head-of-queue, prospecting females can engage in aggressive overthrows at non-natal groups to gain dominance, providing them with an alternative breeding route not

contingent on queue position (Raihani et al., 2010). Indeed, female dispersal may be better predicted by body size and aggressiveness (Raihani, Ridley, Browning, Nelson-Flower, & Knowles, 2008; Ridley & Raihani, 2007b). Overall, these results illustrate the importance of gaining access to a group breeding position for the evolution of delayed dispersal and cooperative breeding, as well as the consequences of group social structure for individual dispersal decisions.

As in many ecological studies of dispersal using complex datasets, we find mixed support for the predictions of the ecological constraints and benefits of philopatry hypotheses (Field, Foster, Shreeves, & Sumner, 1998; Wong, 2010). First, floating carries a high cost for both sexes, and likely limits dispersal, as predicted by the ecological constraints hypothesis (prediction 1A; Ridley et al., 2008). Male dispersal in particular is predicted by ecological constraints:

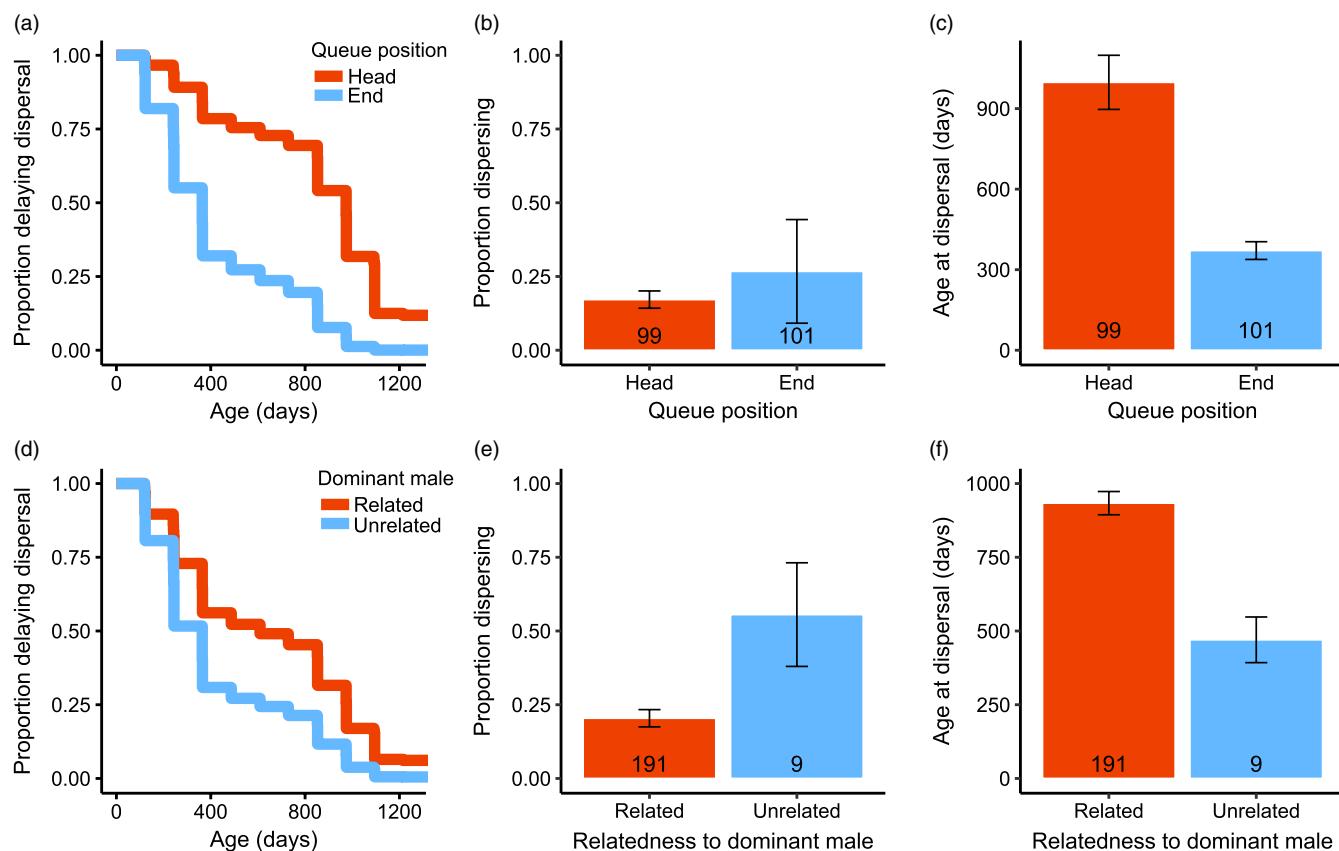


**FIGURE 2** Male dispersal delay probability per season per (a) number of breeding vacancies, (c) rainfall quantile and (e) inter-group distance quantile. Raw data indicating proportion ( $\pm$ SEM) of males dispersing per (b) number of breeding vacancies, (d) rainfall quantile and (f) inter-group distance quantile. Numbers indicate sample sizes. Breeding vacancies, rainfall and inter-group distance are categorized here for illustrative purposes and were continuous variables in our analyses

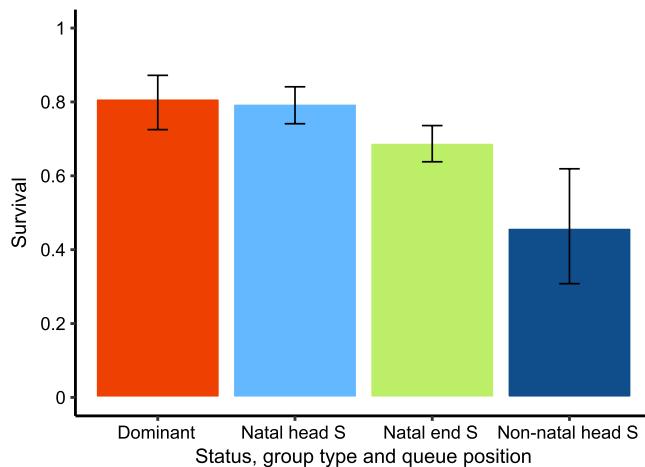
males are more likely to disperse when rainfall is high (prediction 1C) when breeding vacancies are common (prediction 1D), or groups are close together. Newly formed groups consisting of unrelated birds are smaller and much less stable than established groups; group size also affects productivity (Ridley, 2016). Consequently, breeding vacancies in established groups appear to be preferred over formation of a new group, as indicated by the low likelihood of dispersal when more territory becomes available (prediction 1B). Several benefits of philopatry are also important in this system: in natal groups, survival is higher (prediction 2A), higher indirect benefits are available (prediction 2C) and natal subordinate males (but not females) have greater access to future breeding opportunities, accounting for queue position (prediction 2D). However, the ecological constraints and benefits of philopatry hypotheses could not predict female dispersal patterns nor could the role of social circumstances in male dispersal behaviour be predicted. While these theories are valuable in identifying the factors that may promote dispersal, neither on their own nor together did they adequately explain the overall pattern of dispersal observed.

The dual benefits hypothesis incorporates an alternative perspective of the benefits of group-living, encompassing some predictions of the ecological constraints and benefits of philopatry hypotheses, but also considering group size and genetic make-up (Shen et al., 2017). For southern pied babblers, the CA benefits available from

living and breeding in large stable groups are particularly high and likely drive dispersal decisions (predictions 4A–4C, Table 1); RD benefits are not at work (predictions 3A–3C). Males disperse in response to available breeding vacancies within established groups, or improved ecological and social conditions to search for and obtain such opportunities, indicating the high value and pressing need for subordinate helpers (CA; prediction 4A). Females, though mainly free from ecological constraints, disperse from small groups but stay longer in large groups (prediction 4C). Furthermore, groups non-aggressively accept unrelated subordinates until the most productive group size is reached, and immigration pressure is higher on large groups (predictions 4B and 4C; Nelson-Flower, 2010, Ridley, 2016). In fact, very small groups may sometimes even “kidnap” fledglings from neighbouring groups to increase group size (Ridley, 2016). CA benefits are likely to drive group-living behaviour in other cooperatively breeding species. For example, in African mole-rats, small nascent colonies are ephemeral and the extensive burrow system requires coordinated group action for development and maintenance (Faulkes & Bennett, 2016). In hover wasps *Liostenogaster flavolineata*, a new queen is more likely to colonize a vacant nest if it contains an older developing brood (Field et al., 1998). Overall, the dual benefits hypothesis provides predictions and strong explanatory power to understand delayed dispersal and group-living in this species; looking forward, it may be applied



**FIGURE 3** Male dispersal delay probability per season per (a) queue position and (d) relatedness to dominant male. Raw data indicating proportion ( $\pm$ SEM) of males dispersing per (b) queue position and (e) relatedness to dominant male. Raw data indicating mean age ( $\pm$ SEM) at dispersal for males per (c) queue position and (f) relatedness to dominant male. Numbers indicate sample sizes



**FIGURE 4** Survival probability per 6-month period (with 95% confidence intervals) of dominants and various ranked subordinates in natal and non-natal groups. Natal head S = head-of-queue natal subordinate, natal end S = end-of-queue natal subordinate, non-natal head S = head-of-queue non-natal subordinate

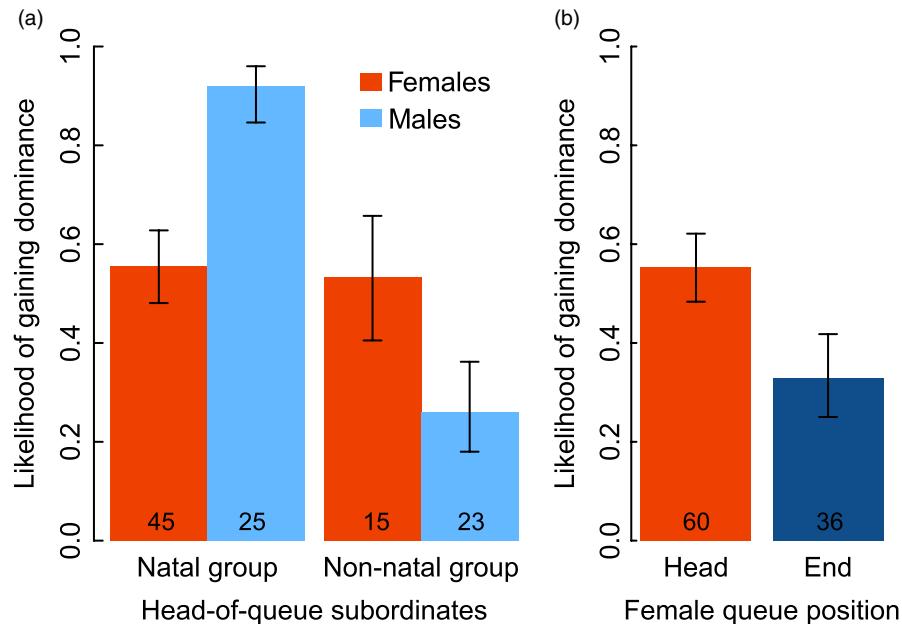
to species occupying a wide variety of ecological conditions, including those in which groups do not arise through philopatry.

Social status (queue position) is a strong determinant of access to a future breeding position and is consequently central to individual dispersal strategy in pied babblers, particularly in males. Reproductive queues also play important roles in other species, such that those lower in the social queue disperse earlier (Ekman, Eggers, & Griesser, 2002), gain lower quality territories (Ens, Weissing, & Drent, 1995), face long waits for territory inheritance (Cockburn, Osmond, Mulder, Double, & Green, 2008) or remain smaller in size (Buston, 2003). Theoretical models developed around the phenomenon of reproductive queues (“queuing theory”) stress the frequency-dependent nature of this strategy: long queues should yield large

benefits, and the fitness outcomes of different queuing tactics should be equal (Pen & Weissing, 2000; van de Pol et al., 2007). In the southern pied babblers, it remains unclear whether equal reproductive payoffs can be gained from early dispersal compared with waiting to become head-of-queue in the natal group, particularly since fates of all dispersing individuals are unknown (Koenig et al., 1996). Given the reduced survival of non-natal subordinates and the high costs of floating (Ridley et al., 2008), it seems likely that early dispersal in babblers could instead “make the best of a bad job” for end-of-queue natal subordinates.

It is important to note that individuals that suddenly dispersed may have been excluded from some analyses or listed as dead, because we could not differentiate these from those that died. Dispersal tends to be short and dispersers often engage in loud displays, making detection appear fairly likely (Golabek & Radford, 2013; Nelson-Flower et al., 2012). However, young floaters may stay silent to avoid detection (A.R. Ridley, unpublished data). As a result of these potential biases, survival in non-natal groups may be under-estimated because these groups are less stable (Ridley, 2016), resulting in lower philopatric benefits than reported here. Social contexts prompting early dispersal (and undetected floating) may have greater impact than reported here.

Social queues also have important consequences for conflict within southern pied babbler groups and potentially for reproductive investment in the sexes. First, because end-of-queue males cannot acquire dominance, dominant males appear to prioritise related males in the queue. Both here and in prior work this reproductive nepotism is evident: head-of-queue subordinate males unrelated to dominant males do not remain in such groups for long (typically weeks), while related subordinate males often stay for considerable periods (typically years) (Nelson-Flower & Ridley, 2016). Similarly, meerkat *Suricata suricatta* dominant females are more likely to evict nieces than daughters, thereby prioritizing close kin in the reproductive queue



**FIGURE 5** Likelihood of dominance acquisition by (a) head-of-queue subordinates in natal and non-natal groups and (b) head-of-queue and end-of-queue subordinate females. Numbers indicate sample sizes

(Clutton-Brock, Hodge, Flower, Spong, & Young, 2010). Second, conflict over head-of-queue benefits appears to favour eviction of brothers by young subordinate males in their natal group. Similar evictions occur in Siberian jays *Perisoreus infaustus* (Ekman et al., 2002) and in group-living fish, although in the latter, queues are size-based rather than age-based (Buston, 2003; Wong, Buston, Munday, & Jones, 2007). Third, lower ranked offspring may suffer decreased fitness as a result of reduced access to future reproductive success, following the “offspring depreciation hypothesis” (Ridley & Sutherland, 2002). This hypothesis suggests that sex ratios may bias towards the non-queuing sex, potentially as a result of differential offspring investment. Sex biases towards females consistent with this prediction appear to occur in this species (Nelson-Flower et al., 2012), but whether these result from differential investment remains to be determined.

In summary, our results demonstrate that recent theoretical developments provide a useful framework for testing the factors affecting delayed dispersal (Shen et al., 2017). Furthermore, we highlight the importance of within-group reproductive social queues for dispersal decisions, and suggest that early dispersal may be a “best of a bad job” alternative mating strategy for individuals with little prospect of gaining future breeding success from remaining within the natal group. Together, these findings further our understanding of the evolution of delayed dispersal, a step that is essential for the formation of familial societies and the evolution of cooperative breeding (Cornwallis et al., 2017; Griesser et al., 2017).

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## AUTHORS' CONTRIBUTIONS

M.N.F. conceived the ideas in discussion with A.R.R., E.W. and T.F.; A.R.R. made data collection possible through extensive habituation of the population; A.R.R. coordinated field data collection and logistics; all authors contributed to collection of data; M.N.F. and E.W. analysed the data and M.N.F., T.F. and E.W. wrote the paper. All authors contributed critically to the drafts and gave final approval for publication.

## DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.517c56h> (Nelson-Flower, Wiley, Flower, & Ridley, 2018)

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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