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Research

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Habitat fragmentation shapes natal dispersal and sociality in an Afrotropical cooperative breeder

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It remains poorly understood how effects of anthropogenic activity, such as large-scale habitat fragmentation, impact sociality in animals. In cooperatively breeding species, groups are mostly formed through delayed offspring dispersal, and habitat fragmentation can affect this process in two opposite directions. Increased habitat isolation may increase dispersal costs, promoting delayed dispersal. Alternatively, reduced patch size and quality may decrease benefits of philopatry, promoting dispersal. Here, we test both predictions in a cooperatively breeding bird (placid greenbul, *Phyllastrephus placidus*) from an Afrotropical cloud forest archipelago. Males born in fragmented forest dispersed about 1 year earlier than those born in continuous forest. Contrary to females, males also started to reproduce earlier and mostly settled within their natal patch. Females only rarely delayed their dispersal for more than 1 year, both in fragmented and continuous forests. Our results suggest that early male dispersal and reproduction is jointly driven by a decrease in the value of the natal territory and an increase in local breeding opportunities in fragmented forest. While plasticity in dispersal strategies of cooperative breeders in response to anthropogenic change is believed to optimize reproduction-survival trade-offs, to what extent it shapes the ability of species to respond to rapid environmental change remains to be studied.

1. Introduction

Group living is a widespread phenomenon occurring in many taxa such as insects, fishes, birds and mammals [1]. One route leading to group living is through delayed dispersal, where offspring remain on the natal territory beyond the dependent period [2,3]. The formation of such family groups is believed to have set the stage for cooperative breeding [3], where some individuals forego the opportunity to breed independently and opt to help raise young that are not their own offspring. In some cooperatively breeding species, social groups may also form through the immigration of unrelated individuals [4].

In long-lived species, delaying dispersal and the onset of reproduction may be an adaptive life-history strategy that maximizes lifetime reproductive success [5–7]. By staying in their natal territory, offspring may receive extended parental care and benefit from access to resources and familiarity with their territory while competing for local breeding opportunities (natal territory as a 'safe haven' [5]). In addition, philopatric offspring can benefit directly from group membership, for example, through improved survival as a result of better

access to, or more efficient exploitation of, critical resources [8–10] or of better protection from predators [11–13]. Group members may also improve their chances of current or future reproduction through acquisition of within- or extra-group parentage [14,15], or by obtaining a dominant position in the natal or in a neighbouring territory [5,16]. Such benefits may also explain why some individuals join non-natal groups as subordinates [17]. Apart from direct fitness benefits derived from group membership, philopatric offspring may also gain indirect (kin) benefits by increasing the fitness of close relatives, for instance, through help with nest protection [18] or food provisioning to nestlings [19].

The decision to delay dispersal, as an alternative strategy to disperse and attempt to breed or ‘float’ in the population until a breeding vacancy becomes available, depends on multiple factors [20]. A high relative value of the natal territory (e.g. high amount of resources in the territory [8,21], the presence of parents [22–24] or a high rank in the social queue for dominance [25]) may promote prolonged philopatry. Extrinsic constraints may also play a role in the decision on the timing of dispersal [20,26]. For instance, low competition for breeding opportunities [21,27], as well as low costs of independent reproduction (e.g. through additional food resources [28]) or movement (i.e. low search costs for breeding vacancies [25,29]) may facilitate the acquisition of an independent breeding position and promote earlier dispersal.

The timing and distance of natal dispersal often differ among sexes. In cooperatively breeding birds, male offspring typically stay longer in the natal territory than females, where they wait for a breeding opportunity in their own territory or a nearby one [30]. Female offspring, on the contrary, typically disperse sooner and farther to occupy a breeding position [30]. This pattern may reflect differences in the fitness pay-off of delayed dispersal between the sexes, such as in the cost of dispersal [29,31] or in the level of competition for mates (e.g. biased sex ratio [32]).

Human-induced environmental changes can be expected to affect the fitness pay-off of delaying dispersal. Anthropogenic activities increasingly result in the global loss, isolation and degradation of natural habitats (henceforth referred to as ‘habitat fragmentation’) [33]. Currently, more than 70% of the world’s remaining forests are prone to human activities, altered microclimate, and the presence of non-forest species that may cause severe habitat degradation [34], and although tropical forests still represent the world’s currently most intact forest landscapes, their fragmentation are predicted to accelerate over the coming five decades [35]. Moreover, negative effects of habitat fragmentation on biodiversity were recently shown to be highest in tropical forests, probably because these ecosystems have been less exposed to large-scale habitat disturbance in their evolutionary past [36]. Anthropogenic-driven changes in the extent, quality and spatial arrangement of tropical forest can be expected to affect the fitness pay-off of delaying dispersal [37] and therefore social group formation, in two contrasting ways. On the one hand, increased isolation of territories as a result of forest fragmentation may increase the energetic and/or predation costs of dispersal [38], which may affect the dispersal strategy of the more dispersive sex in particular. Under such a scenario of increased costs of dispersal, offspring born in more fragmented habitats are predicted to show higher levels of natal philopatry [39]. On the other hand, by decreasing patch size and quality, habitat fragmentation probably

restricts opportunities for local breeding and weakens the value and ‘safe-haven’ function of the natal territory [40]. Such reduction in benefits of philopatry is predicted to promote advanced, rather than delayed, dispersal in the more philopatric sex [20].

Cooperatively breeding species have been shown to be sensitive to the effects of habitat fragmentation, mainly through disruption of dispersal owing to loss of landscape connectivity [41–43], ultimately resulting in local population declines or reduced metapopulation sizes owing to low patch occupancy [44–47]. Alternatively, cooperative breeding strategies could dampen impacts of habitat fragmentation [40,48,49]. For example, cooperative breeding may result in a higher average reproductive success [50] or in a lower level of demographic stochasticity through a reduction in the variance of reproductive success (bet-hedging; [51]). Further, sexually mature subordinates may serve as a pool of potential breeders, meaning that vacant breeding positions are quickly filled (e.g. following the death of a dominant breeder) [52]. Yet, although there is increasing evidence of anthropogenic effects on the expression and evolution of life-history strategies and trade-offs in natural populations [53–55], how, and to what extent, anthropogenic habitat change affects group formation remains poorly understood [39,56].

In this study, we assess how forest fragmentation affects natal dispersal strategies and group formation in a cooperatively breeding bird species (placid greenbul; *Phyllastrephus placidus*) inhabiting an indigenous cloud forest archipelago in southeast Kenya. After assessing how groups form (delayed dispersal versus immigration of non-natal subordinates), we compare dispersal strategies of offspring born in eight subpopulations. Two of these subpopulations inhabiting more continuous and intact indigenous forest (henceforth referred to as ‘continuous forest’) are large (hosting more than 20 territories each, electronic supplementary material, figure S1) and costs of within-forest movements are presumed to be low [57,58] (table 1). Six other subpopulations inhabiting small and degraded forest remnants in the most fragmented section of the archipelago (henceforth referred to as ‘fragmented forest’ which is assumed to be of lower quality [59]), are small (hosting between two and eight territories each, electronic supplementary material, figure S1), and costs of between-territory movement, often involving crossing the heterogeneous landscape matrix, are presumed to be high [57,58] (table 1). We hypothesize that the fitness pay-off of delayed dispersal and reproduction varies with the level of habitat fragmentation. If habitat fragmentation primarily increases dispersal costs, we predict the more dispersive sex (here: females) to delay their dispersal for a longer time in territories located in fragmented forest (i.e. decreased survival of dispersers [26]). By contrast, if habitat fragmentation primarily reduces habitat quality, we predict the more philopatric sex (here: males) to delay their dispersal for a shorter time period in such territories (i.e. decreased survival of residents [26]).

2. Material and methods

(a) Study species and data collection

The placid greenbul is a medium-sized (mean weight: 30.6 g), insectivorous passerine from East Africa’s moist forests with a medium lifespan (oldest individual recorded: 19 years). Data

Table 1. Nest properties in continuous and fragmented forest in the Taita Hills cloud forest archipelago.

	fragmented forest	continuous forest
per cent indigenous forest cover 200 m around nests (mean and [range])	31% [4%; 72%]	80% [25%; 100%]
per cent indigenous forest cover 1000 m around nests (mean and [range])	4% [2%; 7%]	27% [13%; 40%]
number of adjacent nests within 500 m around nests (mean $\pm$ s.d.)	3.10 $\pm$ 2.4	13.8 $\pm$ 5.7
mean distance to the three nearest nests (mean $\pm$ s.d.)	449 m $\pm$ 753	120 m $\pm$ 63

were collected during the breeding season (from November until March) in the indigenous cloud forest archipelago of the Dabida massif of the Taita Hills (30°25' S, 38°12'50' E). Placid greenbuls breed and forage as pairs or in small groups (70% of pairs) in the indigenous forest understory (up to seven individuals, mean group size: 3.1 individuals [60]) where territories are occupied year-round. Dominant pairs generally reneest within the same area in consecutive years (mean $\pm$ s.d. distance between nests: 59 $\pm$ 57 m, 85% of distances were $\leq$ 100 m, n = 177 nests). Typically, two eggs are laid and incubated by the breeding female. In addition to the dominant pair, subordinates of both sexes may provide food (*ca* 40% of subordinates) and offer protection against predators to the nestlings [60].

In our study area, large-scale deforestation started at the beginning of the twentieth century. Airborne remote sensing data showed that half of the remaining indigenous tropical cloud forest was lost between 1955 and 2004 [61]. This severe forest fragmentation has led to a scatter of breeding groups of variable size (subpopulations), largely located within the boundaries of eight indigenous cloud forest remnants ranging in size between less than 1 ha and 120 ha (electronic supplementary material, figure S1) [61,62]. In continuous forest (subpopulations Ngangao and Chawia), the interior is characterized by late-successional tree species, high tree diversity and density, high shrub density, low herb cover and low anthropogenic disturbance. By contrast, small forest patches in the more fragmented, central section of the archipelago are dominated by fewer and smaller trees at lower density that are typically associated with forest gaps and margins and partly mixed with exotic trees. In addition, shrub density is lower, herb cover denser, and disturbance by logging, cattle grazing and fuelwood collection higher than in continuous forest [59,63]. Anthropogenic disturbance also occurs at the edges of the large fragments. Different subpopulations are isolated from each other by gaps spanning at least 500 m of agricultural fields and exotic tree stands (electronic supplementary material, figure S1) [57]. As an understory insectivore, placid greenbuls depend on an intact understory vegetation from which they can glean insects [64]. Accordingly, they appear sensitive to habitat degradation [65] and have suffered a loss of population connectivity over the last century [43], resulting in a positive genetic clustering within the metapopulation [66]. Homing experiments in our study area showed that matrix composition and configuration strongly affect movement patterns in placid greenbuls, with individuals avoiding open and built up areas and selecting indigenous forests when moving through the landscape [57].

During 11 breeding seasons (2007–2019; no data available in 2010 and 2011), placid greenbul nests were monitored in all eight subpopulations. Upon detection, each nest was visited every fourth day until all nestlings had fledged or the nesting attempt failed. Prior to fledging, at around 9 days old, nestlings were individually colour-banded and a blood sample was taken. During nest visits, a combination of focal observations, video-recordings and targeted trapping sessions were used to identify the members of a breeding group and determine their breeding status. Upon trapping, each adult was metal- and colour-banded, aged and a blood and/or feather sample was taken.

Each 'breeding group' consisted of the territorial adult breeding pair (henceforward referred to as 'dominant breeders') and all subordinates (if any) observed at a particular nest. Dominant breeders were identified based on cloacal swellings (males), or on the presence of a brood patch or observed incubation (females). All other individuals present at a nest were assigned as subordinates. Individuals were sexed molecularly using a set of sex-linked primers P2/P8 [67]. Although all suitable indigenous forest fragments were systematically searched for nests during the breeding period, some breeding attempts remained undetected as suggested by the occurrence of unringed juveniles that were trapped each year.

(b) Resighting histories

We constructed resighting histories of 481 individuals that fledged between 2007 and 2017 in fragmented forest (36 males and 42 females) and continuous forest (207 males and 196 females). See the electronic supplementary material, figure S2 for the distribution of resightings of fledglings in relation to their age, state, sex and habitat type. During each breeding season (until 2019), birds that were resighted in a breeding group were classified as 'breeder', 'philopatric subordinate' or 'immigrant subordinate'. A subordinate was considered philopatric when it was resighted together with its presumed mother or father (83 resightings) or when it was never observed farther than 100 m away from its natal nest (13 resightings). Otherwise, it was considered an immigrant subordinate. Individuals that were not resighted were given the status 'unknown fate'. This 'unknown fate' category combined three different cases: (i) individuals that were dead; (ii) individuals that were alive and part of a breeding group as subordinate or breeder, but were not resighted; (iii) individuals that were alive and had dispersed from a breeding group and (temporarily) employed a 'floating' strategy, and were therefore not resighted in a breeding group (electronic supplementary material, figure S3). Because only six individuals were resighted as immigrant subordinates, these were lumped with birds of 'unknown fate' to avoid over-parametrization of the model.

(c) Model description

We constructed a Bayesian multistate capture-mark-recapture model (see the electronic supplementary material, figure S3 for its graphical representation), implemented in the program JAGS [68] with the R package 'jagsUI' [69]. We estimated the following transition probabilities, conditional on individual survival: (i) from philopatric subordinate to non-breeding disperser (i.e. floater or immigrant subordinate), (ii) from philopatric subordinate to breeder, and (iii) from non-breeding disperser to breeder. During 11 breeding seasons we did not observe a single case of a former breeder or immigrant subordinate that subsequently returned to its natal territory as a subordinate. Therefore, we assumed that individuals do not return to their natal territory after dispersal or after gaining a breeding position, and do not become a subordinate or a floater after obtaining a breeding position. Transition probabilities from philopatric subordinate to non-breeding disperser or to breeder were

estimated per sex, age class (from 1 to 3+ year(s) old) and habitat type (degraded versus continuous forest). However, this was not possible for the transition from non-breeding disperser to breeder as this required a larger sample size than was available. Apparent survival probabilities were estimated separately for males and females, for first-year and adult (more than 1 year old) birds and for fragmented and continuous forest. Estimates of first-year survival were similar for males and females within each habitat type. We thus estimated a single first-year survival per habitat type to facilitate estimation of the other parameters. To account for variation in sampling procedure across time periods, three different resighting probabilities were estimated (period 1: 2008–2009; period 2: 2012–2016/2018–2019; period 3: 2017). During 2017, resighting probability differed because video recordings and trapping of adults was only performed during a short period at a restricted number of nests. During 2010–2011, resighting probabilities were set to 0 because no sampling occurred during that period. We assumed similar resighting probabilities for philopatric subordinates and breeders, whereas the resighting probability of non-breeding dispersers was set to 0. Such a multistate formulation with constraints on transition probabilities and time-constant survival probabilities allowed the estimation of state-transition probabilities from and to unobservable states [70]. We used vague priors for all estimated parameters (i.e. uniform or Dirichlet distributions depending on the parameters). We ran four Markov chain Monte Carlo chains initiated at random starts for 50 000 iterations. We discarded the first 30 000 samples as burn-in resulting in 80 000 drawn samples from the posterior distributions. The R script is presented in the electronic supplementary material, S4. We determined model convergence and parameter extrinsic redundancy [71] by examining trace plots and by comparing prior and posterior distributions. As transition probabilities of philopatric subordinates were not estimable for 3+ year old individuals from fragmented forest, we here assumed the same probabilities as for 2 year old individuals. This assumption does not affect the main conclusions derived from the model (electronic supplementary material, S5).

Owing to the small number of resighted individuals, particularly in fledglings from fragmented forest (electronic supplementary material, figure S2), we performed a sensitivity analysis where we added to the dataset 60 subordinates, aged during their initial encounter as 1 year old individual and assumed to be philopatric (electronic supplementary material, S6). Inclusion of these individuals resulted in similar posterior estimates of the parameters of interest. We also performed simulations (bootstrap resampling among continuous forest data with sample sizes as small as in fragmented forest) to assess the robustness of our results (electronic supplementary material, S7).

Because differences in adult survival rates between individuals from fragmented and continuous forests could not be estimated with high precision in this model (table 2), we estimated survival rates in fragmented and continuous forests in a separate model where we used data on dominants only (electronic supplementary material, S8). For this analysis, we were able to include more individuals (i.e. not only fledglings but also individuals first captured at later ages), while model parametrization was considerably reduced as transition probabilities between different states did not need to be estimated.

3. Results

Among 105 fledglings resighted at least once (out of 481, 22%), 77 (73%) were resighted as philopatric subordinates during at least one breeding season. Four female and two male fledglings (6% of all resighted fledglings) were resighted

as subordinate members of a non-natal breeding group. Forty-one fledglings (39% of all resighted fledglings) settled as breeders (see below). Two fledglings were both resighted as philopatric and immigrant subordinates and 15 as philopatric subordinates and breeders. Finally, one fledgling was resighted in all three categories over the study period. The earliest age of settlement of a fledgling was 2 years in fragmented and 3 years in continuous forest (electronic supplementary material, figure S2). Among 1 year old subordinates not ringed as nestlings ($n=60$, electronic supplementary material, S6), 14 settled as breeders. Natal dispersal distances of individuals observed as breeders within continuous forest were larger for females than for males (median $\pm$ median absolute deviation: 1012 ± 526 m versus 163 ± 65 m from their natal territory; $n=15$ and 24 , respectively; figure 1). Two additional females born in continuous forest obtained a breeding position in a subpopulation within fragmented forest (5856 ± 1857 m). Four out of five females born in fragmented forest settled in a different subpopulation (overall median natal dispersal distance: 2000 ± 2340 m), while most males (8 out of 9; 89%) settled within their natal subpopulation (65 ± 55 m). One male dispersed 3251 m to gain a breeding position in a different subpopulation (figure 1).

Multistate capture–mark–recapture modelling showed that most fledglings delayed their natal dispersal for at least one breeding season (figure 2*a,b* and table 2). The time during which dispersal was delayed, however, varied among sexes and with the level of fragmentation. In continuous forest, males delayed dispersal for on average 2 years [1.4; 2.6] (mean [95% highest posterior density (HPD) interval]) while females remained on average 1.1 years [0.8; 1.6] in their natal group. When estimating dispersal timing separately in the two replicate subpopulations from continuous forest (electronic supplementary material, S10), we found that these estimates were similar in both subpopulations (males in Chawia: 1.8 [1; 2.6] years, males in Ngangao: 1.9 [1.2; 2.7] years, females in Chawia: 1.1 [0.6; 1.6] years, females in Ngangao: 1.1 [0.5; 1.7] years). The longest observed delay was 5 years in males and 2 years in females (electronic supplementary material, figure S2). These patterns were markedly different in fragmented forest. Here, differences in delayed dispersal between the sexes were less pronounced and males, in particular, delayed their dispersal for a shorter period than in continuous forest (figure 2*a,b*). Mean time of delay in fragmented forest was 1.1 years [0.4; 1.9] for males and 0.8 years [0.3; 1.3] for females. The longest observed delay was 2 years in males and 1 year in females (electronic supplementary material, figure S2). Male subordinates from fragmented forest obtained a breeding position earlier than those born in continuous forest (4.0 [2.6; 5.4] versus 5.6 [4.7; 6.4]) (figure 2*c* and table 2), while there was less difference for female subordinates (5.0 [3.7; 6.3] versus 5.3 [4.3; 6.2]) (figure 2*d* and table 2). Males as well as females had a relatively high probability to become a non-breeding disperser before obtaining a breeding position (parameter ψ_{12} in table 2; electronic supplementary material, figure S11), both in subpopulations from continuous and fragmented forest. Finally, apparent annual survival of both male and female dominants was higher in continuous (males versus females: 0.77 [0.73; 0.81] and 0.80 [0.76; 0.84]) compared to fragmented (0.68 [0.56; 0.80] and 0.73 [0.62; 0.82]) forest (electronic supplementary material, S8).

Table 2. Posterior mean and 95% HPD interval of parameters estimated by the multistate capture–mark–recapture model. (Ψ_{ij} is the annual transition probability from state i to state j (1, philopatric subordinate; 2, non-breeding disperser; 3, breeder; electronic supplementary material, figure S3). $\Psi_{22} = (1 - \Psi_{23})$. $\Psi_{11} + \Psi_{12} + \Psi_{13} = 1$.)

posterior mean [95% HPD interval]					
parameters	habitat type	sex	age		
			1	2	3+
(a) transition probabilities					
Ψ_{11}	fragmented	male	0.72 [0.43; 0.98]	0.33 [0.06; 0.62]	0.33 [0.06; 0.62]
		female	0.67 [0.34; 0.97]	0.15 [0.00; 0.41]	0.15 [0.00; 0.41]
	continuous	male	0.83 [0.65; 1.00]	0.83 [0.65; 0.99]	0.41 [0.25; 0.59]
		female	0.84 [0.63; 1.00]	0.31 [0.09; 0.56]	0.15 [0.00; 0.42]
Ψ_{12}	fragmented	male	0.20 [0.00; 0.48]	0.30 [0.00; 0.63]	0.30 [0.00; 0.63]
		female	0.26 [0.00; 0.59]	0.73 [0.40; 0.99]	0.73 [0.40; 0.99]
	continuous	male	0.14 [0.00; 0.33]	0.13 [0.00; 0.31]	0.43 [0.18; 0.66]
		female	0.14 [0.00; 0.35]	0.65 [0.38; 0.89]	0.50 [0.07; 0.88]
Ψ_{13}	fragmented	male	0.09 [0.00; 0.24]	0.36 [0.05; 0.69]	0.36 [0.05; 0.69]
		female	0.07 [0.00; 0.20]	0.12 [0.00; 0.36]	0.12 [0.00; 0.36]
	continuous	male	0.02 [0.00; 0.06]	0.04 [0.00; 0.11]	0.16 [0.01; 0.34]
		female	0.03 [0.00; 0.08]	0.05 [0.00; 0.14]	0.35 [0.02; 0.74]
Ψ_{23}	0.18 [0.05; 0.33]				
(b) apparent survival probabilities					
			first year	adult	
	fragmented	male	0.43 [0.23; 0.65]	0.83 [0.67; 0.99]	
		female	0.43 [0.23; 0.65]	0.75 [0.56; 0.95]	
	continuous	male	0.36 [0.26; 0.46]	0.89 [0.83; 0.95]	
		female	0.36 [0.26; 0.46]	0.78 [0.67; 0.90]	
	sampling period				
(c) resighting probabilities					
	2008–2009	2010–2011	2012–2016 and 2018–2019	2017	
	0.31 [0.13; 0.50]	0.00 [0.00; 0.00]	0.56 [0.46; 0.66]	0.45 [0.29; 0.60]	

4. Discussion

In this study of a facultative cooperative breeder from an Afrotropical cloud forest archipelago, breeding groups were predominantly formed through delayed offspring dispersal. Most offspring delayed their dispersal for at least 1 year. In continuous forest, males delayed their natal dispersal for a longer period of time than females, a pattern observed in most cooperatively breeding birds [72]. In fragmented forest, however, males left their natal territory on average 1 year earlier, resulting in a more similar dispersal timing between sexes. Survival rates of dominants were highest in continuous forest.

Individuals of species with a medium (such as the placid greenbul) to long lifespan, are predicted to adjust their dispersal and reproductive strategies to local environmental conditions in ways that maximize their lifetime reproductive success [20,26]. Tropical forests, characterized by low variability in temperature and predictable seasonality in rainfall, represent productive, benign environments [73] that are believed to have favoured the evolution of family living, a

pre-requisite to cooperative breeding [3]. As most greenbul offspring delayed their dispersal for at least one breeding season, both males and females appear to benefit from a ‘safe-haven’ function of their natal territory, even when of low quality [5,6]. Such a pattern may reflect high costs of dispersal or reproduction for young, inexperienced birds [7] or may be owing to extended parental care provided by dominant group members [23,74] as an incentive for offspring to remain in their natal territory until the next breeding season. Dominant breeders may benefit from the presence of subordinates, e.g. in the form of enhanced reproductive success [18,19,50]. In support of this, earlier studies in the same population revealed higher fledgling success and post-fledgling survival in larger cooperative groups, most likely owing to communal predator defence [60,75]. Theoretical models have suggested that such increased reproductive success in larger groups may explain why unrelated subordinates (e.g. non-natal immigrants) are tolerated in cooperative groups [17]. Related subordinates, in turn, may gain indirect fitness benefits from helping with food provisioning and predator defence [76]. The facts that (i) delayed dispersal was also

Figure 1. Dispersal distances between the natal and the breeding territories of 41 individuals ringed as nestlings and 14 ringed when 1 year old (electronic supplementary material, S6). Labels on the x-axis denote the subpopulation where the natal territory was located. When dispersal occurred outside the boundary of the natal indigenous forest, the name of the subpopulation where breeding occurred, is indicated next to the dot. Filled dots, males; open dots, females.

Figure 2. Age-specific cumulative probabilities to delay dispersal (*a,b*) and to obtain a breeding position (*c,d*); for males (*a,c*) and females (*b,d*) (conditional on individual survival). Dots represent posterior mean and shaded areas denote 95% HPD intervals. These probabilities are derived from estimates in table 2 and calculations are presented in the electronic supplementary material, S9. (Online version in colour.)

observed in individuals that were unrelated to the dominant pair (because of extra-pair paternity and death of the mother; [76]), and (ii) a number of offspring joined other breeding groups as subordinate members, suggests that placid green-buls also gain direct benefits from group living, such as

access to resources or collective predator defence. Finally, one female immigrant was observed to gain a dominant position in a non-natal breeding territory, providing (anecdotal) evidence that joining a non-natal group as a subordinate may represent an alternative route to reproduction in this species.

While delayed dispersal occurred both in continuous and fragmented forests, male offspring delayed their dispersal for a shorter period when born in the latter, and dominant breeders also showed lower survival rates in this habitat type. These combined observations suggest that habitat degradation in fragmented forest [59,77] decreases the benefits of delayed dispersal [26], for instance, through a reduction in the amount of resources that can be shared in a group and/or in the level of tolerance by the adult breeders [17,74]. Low territory quality, such as reflected by a scarcity of food resources, has been associated with advanced dispersal in several cooperative breeders [8,21,78] and probably constitutes an important driver of natal dispersal strategies. Moreover, in our study area, territories located in fragmented forest were often surrounded by inhospitable habitat (electronic supplementary material, figure S1; table 1). This probably entailed additional energetic [79] and/or predation costs during daily foraging movements, which may have further contributed to lower breeder survival [80]. Owing to the correlative nature of our study and the limited number of replicates, we currently cannot disentangle the various habitat features that may affect natal dispersal strategies in our study species. Measuring ecological and social properties at the territory level, in combination with food provisioning and removal experiments, may help to understand the drivers underlying delayed dispersal in human-modified landscapes such as the Taita forest archipelago. While changes in natal dispersal strategies are expected to affect sociality and cooperative breeding [8,21,39], an earlier study in the same area did not detect direct relationships between the degree of habitat fragmentation and the occurrence, number and proportion of (helping) subordinates in placid greenbul breeding groups [60].

While subordinate males born in fragmented forest were expected to disperse outside their natal areas to obtain an independent breeding position, they mostly settled within their natal subpopulation (figure 1). We propose two non-mutually exclusive explanations for this pattern. First, we observed that the survival of dominant breeders was lower in fragmented forest and that males born in this habitat type started breeding sooner than those born in continuous forest (figures 1 and 2). This pattern suggests that local breeding vacancies arise frequently owing to high breeder turn-over and are quickly filled by non-breeding individuals. Such a pattern further illustrates how low survival of territorial individuals may affect offspring dispersal both directly, by decreasing the value of the territory, and indirectly, by decreasing habitat saturation (see fig. 5 in [26]). Second, the proportion of long-distance natal dispersal events (11%, $n=9$) may have been underestimated owing to lower survival of dispersing males or lower resighting probabilities thereof. In support of this, long-term capture-recapture data from our study area show that male between-fragment movement occurs at higher rates when originating from fragmented compared to continuous forest (6% versus 0.4% of all recorded movements; $n=185$ and 954 , respectively) (L. Lens 2020, unpublished data). Higher rates of movements and a non-null probability of becoming a non-breeding disperser when born in fragmented forest (table 2; electronic supplementary material, figure S11) suggests that earlier reproduction in this habitat type results from a different fitness pay-off of delaying dispersal and reproduction as compared to continuous forest, and is not solely a response to increased breeding opportunities.

When dispersing beyond the boundary of their natal forest fragment, individuals generally travelled long distances across heterogeneous habitat to find a suitable breeding vacancy

(figure 1). Such movements may not be free of costs, which probably explain why almost 90% of resighted male and female fledglings settled within their natal fragment. The fact that females more likely obtained a breeding position in a non-natal fragment than males, despite potential breeding opportunities within their natal one (see also [41]), either reflects a predisposition of females to leave their natal neighbourhood [81], sex-specific dispersal costs [29], or both. Energetic costs related to dispersal in fragmented landscapes [79] probably affect individual lifetime reproductive success [82] and long-term population persistence [83]. In support of this, females of the cooperatively breeding Florida scrub-jay (*Aphelocoma coerulescens*) born in more isolated territories dispersed both sooner and over longer distances [56], and had a lower reproductive success, compared to short-distance dispersers [42]. Whether, and to what extent, this is also the case in placid greenbuls, remains to be studied.

In conclusion, while it has been argued that cooperative breeders, with their low reproductive rates and restricted dispersal, may be particularly vulnerable to habitat fragmentation [40], we here show evidence for plasticity in natal dispersal strategies that may allow individuals of such species to optimize their reproduction-survival trade-off under rapidly changing conditions [84]. In general, such expression of behavioural plasticity may help mitigate adverse effects of anthropogenic disturbance, as it allows rapid and reversible responses to changing conditions [84]. However, if habitat fragmentation becomes more severe, delayed dispersal may be reduced to the point that it disrupts family living and cooperative breeding. As cooperative breeding may buffer the population against adverse conditions [73,85], this may in turn compromise its ability to cope with rapidly changing environmental conditions.

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Data accessibility. Data analysed in this paper are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6wwpzmvmv> [86].

Authors' contributions. L.C. analysed the data and drafted the manuscript. D.V.L. and B.A. collected the data. M.G. facilitated data collection. L.L. and E.M. designed the study and, together with M.H., helped draft the manuscript. All authors critically revised the manuscript and gave final approval for publication.

Competing interests. We declare we have no competing interests.

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