รายงานฉบับสมบูรณ์

การศึกษาการย้ายอาณาเขตของลูกนกปรอดโอ่งเมืองเหนือ (*Alophoixus pallidus*) โดยใช้วิทยุติดตามตัว

Juvenile dispersal of Puff-throated Bulbul (*Alophoixus pallidus*) using Radio telemetry

โดย

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ทุนสนับสนุนการวิจัย ประจำปีงบประมาณ พ.ศ. 2552-53

ที่จัดรูปแบบ: แบบอักษร: 24 พ., แบบอักษรภาษาที่ซับซ้อน: 24 พ.

ที่จัดรูปแบบ: แบบอักษร: 24 พ., แบบอักษรภาษาที่ซับซ้อน: 24 พ.

SUMMARY

~~Tropical passerines are expected to have higher survival rates than those in temperate zones, though post-fledging survival has rarely been quantified. It is predicted that cooperative breeding species would have even higher rates of juvenile survival because of increased care by adults, but there are few data available on such species. We studied post-fledging survival of the cooperatively breeding Puff-throated Bulbul *Alophoixus pallidus* in an evergreen forest in northeastern Thailand during three breeding seasons (2006-2008). Cumulative probability of surviving the first eight weeks post-fledging was high (0.67 ± 0.01 SE). The mean survival estimate during the first week after fledging was 0.78 ± 0.08 while the mean seven subsequent weeks' survivorship was 0.98 ± 0.01. Survivorship did not vary among years or by sex. Greater nestling weight 2-3 days prior to fledging led to higher survival during the first week, but had no effect after this. Birds fledging earlier in the year survive better than those fledging later, and the presence of helpers contributes nominally to increased fledgling survival during the first week but not thereafter. Understanding factors influencing post-fledgling survivorship provides insights to this limiting life history stage which is typically characterized by high mortality and which impact population dynamics. The survivorship of fledglings reported here adds to the body of evidence that tropical passerines generally experiences higher post-fledgling survivorship than do temperate species. However, fledglings from cooperative breeders may not experience significantly higher survivorship than those from non-cooperatively breeding birds in the same system.~~

While natal dispersal can have a significant impact on population dynamics particularly for cooperative breeders, it is typically difficult to quantify. We modelled probabilities of staying in the natal territory and timing of dispersal in juvenile under the effects of social factors including sex, group size, and presence of helpers. The best fitting model indicates that juvenile birds did not disperse until the second calendar year, at the beginning of and during the breeding season following the hatching year. Dispersal was strongly female-biased both in frequency and distance. Most females dispersed away from their natal territories (94.4%),~~-~~ median number of territories crossed (excluding philopatric birds) ± interquartile was 3.9 ± 1.9 territories~~crossing 2-7 territories (mean 3.4 ± 1.3 SD)~~. Half of the males remained on the natal site as helpers in their second year, while 50% dispersed, 25% of which moved to neighbouring territories. Dispersing female offspring were not influenced by any of the social variables measured, while the presence/absence of helper(s) influenced both timing of dispersal and the probability of staying for males. Using radio telemetry to study natal dispersal of small passerines that exhibit delayed dispersal is not recommended. This problem was due to the life span of

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the battery is relatively short while timing of natal dispersal is unpredictable. Furthermore, catching targeted juvenile for fixing the radio was extremely time consuming and difficult. However, radio telemetry maybe useful tool to study their movement prior to dispersal, which is more practical for small birds in dense vegetation. Our findings of natal philopatry in males and sex-biased dispersal contribute to a growing body of literatures that suggests a range of complex behaviours influence the dispersal patterns of cooperatively breeding birds.

1. INTRODUCTION

Dispersal is a major event in a bird's life as it is a key transition period from non-breeding to breeding status (Woolfenden and Fitzpatrick 1984, Brown 1987). This complex process involves a combination of individual decisions on when, where, how far, or even if to disperse (Wiens et al. 2006). The transition period is particularly important in the complex dynamics of cooperative breeding species, where some individuals may remain in their natal territory for several months post- fledging, some remain philopatric indefinitely (e.g. Pasinelli and Walters 2002, Cockburn et al. 2008, Woxvold and Mulder 2008), and others disperse shorter or longer distances (Eikenaar et al. 2008).

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Data on dispersal and recruitment of juvenile birds are rarely reported in Asia, and no published worked on this topic has been produced in Thailand. Juvenile dispersal is of particular importance as dispersal often has a significant impact on population dynamics. Almost nothing is known of bulbul survival and dispersal behavior, although they are the most common bird family living in any kind of forest habitat in Thailand. Most dispersal studies have been conducted on larger carnivorous birds (e.g. Belthoff & Ritchison 1989, Miller and Smallwood 1997, Ganey et al 1998, Wiens et al 2006), insectivores (e.g. Drilling and Thompson 1988, Baker et al 1995, Dingemanse et al 2003) and waders (e.g. Reed and Oring 1993, Robinson and Oring 1997).

The Puff-throated bulbul (*Alophoixus pallidus*) is a particularly important species because of its capacity as a seed disperser, dispersing at least 98 plant species ~~(Wangworn et al. 2011)~~ and the fact that it is a very abundant bird species in evergreen forest (Khao Yai Project 2006). Puff-throated Bulbul also has the unusual behavior in that it is a cooperative breeder, whereby 1-4 adults in addition to the parents help care for offspring (Pierce *et al*. 2007). There is insufficient data to determine whether these helpers are offspring of the current breeding pairs or they have moved from other neighboring groups. Based on preliminary territory maps, available habitat seems to be limited and this species may be restricted to largely intact evergreen forest, and therefore maybe useful as habitat indicators. Limited suitable habitat might be an ecological constraint forcing juveniles birds stay with

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their parents 7-12 months after they are capable of finding food independently, the time when juveniles of most other species disperse away from their parents. Most of the marked juveniles from the previous years (2003-2005) are of unknown fate because they have not been detected in the study area since they have fledged. They are assumed to have either dispersed outside the plot away from their parents or dead, but there is no available data for this species because dispersal distances appear to be commonly > 500 m and thus the probability of re-locating these juveniles again by random searching is low (Wangworn unpubl). However, because cooperative breeding supports the idea of delayed-dispersal (e.g. Retepro et al 1998, Caffrey 1992), some juveniles can probably stay with parents while others disperse (Woolfenden & Fitzpatrick 1984). To understand the complicated social system of the Puff-throated Bulbul and their population dynamics, we need to investigate the basic life history of juveniles including survival and dispersal which is one of the most critical times of a bird's life (Woodward & Woodward 1979).

Some of the hypotheses that have been proposed to promote cooperative breeding life strategies include habitat saturation, kin selection and the life history hypothesis. The habitat saturation hypothesis suggests that in habitats with a high density of conspecifics a selective advantage is conferred to those who do not have an opportunity to breed, by assisting the reproductive efforts of others (Komdeur 1992). Kin selection confers a selective advantage by assisting in the raising of offspring for closely related individuals and thereby ensuring some genetic contribution (e.g. Cockburn 1998, Baglione et al. 2003). Kin selection links to the benefits of philopatry whereby living at home provides a safe place to queue for breeding vacancies and confers an advantage through familiarity with the natal area and neigbourhood (e.g. Kokko and Ekman 2002, Pasinelli and Walters 2002, Cockburn et al. 2008). It also improves survivorship via group alarm calling and anti-predator behaviour (Brown 1987, Griesser 2003). The life history hypothesis suggests that cooperative breeding is a consequence of increased longevity and slow territory owner turnover, which consequently limits juvenile dispersal (Arnold and Owens 1998, 1999, Hatchwell and Komdeur 2000).

While juvenile birds of most passerines disperse within their fledging year, delayed dispersal (whereby young birds remain on the natal territory until some later period) occurs in a small proportion of species. Delayed-dispersal is regularly observed in cooperative or social breeding species (e.g. Ligon and Ligon 1990, Caffrey 1992, Koenig et al. 1992, Restrepo and Mondragón 1998). In some cases, juveniles remain with their parents as helpers (e.g. Woolfenden and Fitzpatrick 1984, Cockburn 1998, Pasinelli and Walters 2002), although delayed dispersal is not always associated with helping (e.g. Gayou 1986, Ekman et al. 1994, Kokko and Ekman 2002). In other cases, juveniles may remain on the natal territory for months to years before dispersing long or short distances to occupy breeding vacancies as they occur.

Sex differences in natal dispersal usually occur in species living in permanent social groups (Pusey 1987). Dispersal in most birds is female-biased (e.g. Greenwood 1980, Clarke et al. 1997), and is generally explained as a strategy to avoid inbreeding (e.g. Greenwood 1980, Perrin and Mazalov 1999, Daniels and Walters 2000, Komdeur et al. 2008). Thus the majority of helpers are sons from previous broods (Doerr and Doerr 2006, Cockburn et al. 2003, 2008). The general explanation is that staying at home as a 'safe haven' would benefit young males by increasing survival (e.g. Rowley and Russell 1997, Kokko and Ekman 2002). Natal philopatry also results in increasing familiarity with resources and facilitates territory defence (Miller and Smallwood 1997, Perrin and Mazalov 1999) while increasing chances of detecting breeding vacancies around the natal area (Cockburn et al. 2003). However, this does not entirely explain female biased philopatry (Caffrey 1992) or cases where both males and females are equally philopatric (Ligon and Ligon 1990, Ekman et al. 2002, Woxvold et al. 2006).

We investigated philopatry of juvenile Puff-throated Bulbuls (*Alophoixus pallidus*) which have been recently shown to breed cooperatively and non-cooperatively in the same population (Pierce et al. 2007; Sankamethawee et al. 2009). Hence, this study system provides a unique opportunity to increase our understanding of complex social systems in tropical passerines. We evaluated ecological models from mark-resighting data to explain survival probabilities of fledgling and probability of remaining within the natal territory as well as the timing and distance of dispersal particularly in the presence or absence of helpers to provide a broader understanding of the role of group living system and natal dispersal patterns in influencing kin structure and population dynamics of cooperatively breeding birds.

2. OBJECTIVES

1. To investigate juvenile movements during the period before dispersal of Puff-throated Bulbul (PBU) both on a spatial and temporal scale.
2. To investigate how sex and age influence dispersal patterns of Puff-throated Bulbul.
3. To investigate how cooperative breeding in birds may have evolved with habitat saturation.
4. To investigate how juvenile survival during the first year influences population and social structure of PBU in subsequent years.

3. METHODS

Study site

The study was conducted in Khao Yai National Park, northeastern Thailand (14°26′ N, 101°22′ E) on the 30 ha Mo-Singto long-term biodiversity research plot (Figure 1; Brockleman 1998) (hereafter MST). The plot is situated in mature, seasonally-wet evergreen forest with undulated ridges and valleys, elevation 723–817 m asl (Brockelman 1998). Most part of the plot is undisturbed primary forest except for a 20 x 120 m strip of approximately 40-year-old secondary forest at the northern edge of the plot. The average annual rainfall is 2,326 mm, most of which falls between May and October (Kitamura *et al*. 2002). The vegetation is dominated by evergreen trees viz. *Ilex chevalii*, *Cinnamomum subavenium*. The canopy layer is at approximately 30-35 m, with some emergent trees of more than 40 m e.g. *Dipterocarpus graciliis*, *Cinnamomum illicoides*. The lower story is dominated by *Polyalthia evecta* and Rattans (*Daemonorops sp. and Calamus sp.*) which are common along the wet and gully areas.

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Study species

Puff-throated bulbul *(Alophoixus pallidus*) family Pycnonotidae, is a medium-sized bird (37-54 g). It is a resident in understorey and mid canopy level of evergreen forest. Bulbuls mainly are highly frugivores (Corlett 1998, Sankamethwee et al. 2011) and can be found in nearly every terrestrial habitat in Thailand. Many species are tolerant of habitat disturbance (Corlett 1998), but Puff-throated bulbuls are mainly found in evergreen forests which probably indicates their sensitivity to forest degradation.

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Field methods

Mist-netting– and individuals' marking- Mist-nets were set to catch adult birds and free-flying juveniles. All captured birds were weighed, measured (wing and tail length), and their body condition examined. All captured Puff-throated Bulbuls were ringed with unique color ring combination of 2 colors and one Royal Forest Department (RFD) aluminum ring with a unique number. Nestlings at the age of about 8 days (3-4 days before fledging) were also ringed to determine it's origin on future encounters.

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Group structure and location- Every territory in and adjacent to the MST plot was mapped (Figure 2) by following marked individuals and recording foraging locations and encounters with other groups

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(Carmen 2004, Woolfenden & Fitzpatrick 1984). Every surrounding territory in the study tract (in and adjacent to the MST plot) was checked monthly to determine the members of each group and number of individuals.

Nest finding, nests distribution, breeding activities- Nests of all breeding groups were searched for during the breeding season (February-July)**.** Nests were checked every 2 days for hatching, eggs and nestling survival until fledging day. Positions of fledged nests were defined as the origin point of juveniles (Ganey *et al* 1998). All attempted nests (failed and successful) of each breeding pair were mapped. Nest success was analyzed using the Mayfield method (Mayfield 1975).

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Post-fledging survival - All active nests were checked regularly (every 3 days in the nestling stage) until fledging or failure. Fledging date was defined as day 0. After day 0, fledglings were monitored once a week until the week 8. Although the fledglings started to feed partly independently at the age of about 3-4 weeks, they still begged for food from adults until weeks 6-7. Thus, even after this 2 months period the juveniles still remained with their parents, but they were assumed to feed independently from their parents. Fledglings from each group were search for up to two hours due by thoroughly searching the whole territory. Resighting histories for seen birds were recorded as 1 and 0 for not seen. Some successful nests were not found until the day of fledging and so those fledglings were unringed but could still be identified from the adults until the end of their post-juvenile moult. When they were full-grown, these unringed juveniles were distinguished from adults by bill colour and the contrast of new and old wing feathers. The bill colour of juveniles is pale yellow while greyish in adults. Plumage colour of adults is uniformly olive-brown whilst juveniles are browner with no olive tones.

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Radio tagging - During mist-netting session, if any juvenile Puff-throated bulbul was caught in addition to the color rings, it tagged with a radio transmitter. We used the transmitters model BD-2 of 1.3 g (2 % of body weight) (Holohil system (Canada)). The transmitter was fitted by using backpack harness method. The weight of transmitter was approximately 4% of the body weight of the birds (Peh and Ong 2002). Puff-throated bulbuls weight about 40-50 g, then Lifespan of the battery is typically 28-50 days, dimensions (LxWxH) 15 x 7 x 3.5 mm. Pulse width 22 ms ± 10%, pulse rate nominal 0.67 p/s (40 p/m).

Dispersal and settlement pattern- After two months, all known juveniles were followed until the next breeding season to locate their new territories or record the group composition if they remained on their natal territory. Dispersal distance was defined as the distance between hatching site and new settlement area (Halliburton & Mewaldt 1976). The study area was extended 400 m in 4 directions (North, East, West, and South) outside the core 30 hectare permanent plot (Figure 3) with the aim of searching for dispersing individuals. Randomized area searches were conducted on at least 25 % of each of the extended areas around the MST plot. Two observers were applied to this survey to improve detection rates and to facilitate following of any groups encountered in order to identify ringed birds. The surveys were conducted twice in the breeding season and twice in the non-breeding season.

Radio- tracking and range analysis- Radio tracking techniques involves following individual birds on foot using hand-held 3 element Yaki antenna. Portable R-1000 receiver from Communication specialist Inc. was used. Homing techniques was applied to locate the position of tagged juveniles. Each individual was followed once a day to get locations of movement. Positions or locations of the bird were recorded using GPS. The tagged birds will be followed until they loose the transmitter or the birds settle in a fixed territory as pair or new group in the subsequent breeding season. The birds which leave their natal sites permanently and join new group will be defined as having dispersed. Dispersal distance will be defined as the distance between hatching (natal) site (nest location) and new settlement area (Halliburton & Mewaldt 1976).

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4. DATA ANALYSIS

4.1) Model development

We tested survivorship of 41 juveniles (35 known sex, 6 unknown sex) by modelling monthly survival probabilities during the first year calendar after juveniles were nutritionally independent from parental care using MARK 5.1 (White and Burnham 1999, Cooch and White 2008). Six monthly encounter histories from July-December of each year were analyzed. Survival probability, Φ, is defined as the probability of a juvenile surviving from one month to the next, whether or not it was resighted. Resighting probability, *p*, is the probability that bird will be resighted given that it is alive (Cooch and White 2008). The best fitting model $\Phi(.)\ p(.)$ indicated that juvenile survival remained constant over time since juveniles become nutritionally independent from parental care until completion of their first

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calendar year. Based on model averaging, the survival rate of juveniles older than two months post-fledging was 0.99 ± 0.01 SE, 95% CI 0.95-1.0 up until the subsequent breeding season.

MARK assumes that disappearance of a bird is due to death (Cooch and White 2008). However, because we find that birds surviving more than two months after fledging experience 99% survivorship until the end of the calendar year, we assume the initial disappearance of a bird during their second calendar year is due to dispersal, as there is no reason to presume death suddenly occurs after the new calendar year and the breeding season begins shortly thereafter. We examined the cumulative survival probability from two months post-fledging until the end of the subsequent breeding season (roughly from the beginning of August of their first calendar year until the end of July in their second calendar year), as equivalent to the probability of remaining in the natal territory during this period of the lifecycle.

We tested goodness-of-fit (GOF) for each dataset of different variables by simulating a parametric bootstrap (1000 simulations) from the global model. The variance inflation factor ($\hat{c}$) was calculated as the observed deviances (global model deviance) divided by expected deviance simulated from parametric bootstrapping. Akaike Information Criteria corrected for small sample size (AIC_c) values were adjusted to allow for the extent of overdispersion, measured by $\hat{c}$, to derive a quasi-likelihood (QAIC_c).

We estimated the probability of surviving and resighting to fit the Cormack-Jolly-Seber model in program MARK 5.1. The best-fitting model has a $\Delta\mathrm{QAIC}_c$ of zero (Lebreton et al. 1992), while other models are expressed as some difference ($\Delta\mathrm{QAIC}_c$) from zero. Models with $\Delta\mathrm{QAIC}_c \leq 2$ are equally parsimonious to the best-fitting model (Lebreton et al. 1992, Cooch and White 2008). We use QAIC_c weights to determine the relative likelihood of a model of interest in the set of candidate models.

We tested all possible time-dependent models by designing a parametric index that included monthly intervals, bimonthly intervals, year intervals, and breeding season intervals. The breeding season interval was the one most supported by the data, thus we applied the breeding season intervals to all data sets. We defined; (1) five one-monthly intervals from August-January represented the non-breeding season after hatching (nbr); and (2) six one-monthly intervals from February-July represented the first breeding season after hatching (br). All variables (sex, group size, and presence/absence of helper) were tested in the model in relation to (1) the probability of staying in the natal territory and (2) the timing of dispersal.

We tested timing of dispersal of known sex juveniles (n = 35). Sexes were separated (18 females, and 17 males) to determine whether any sex bias was evident in dispersal versus philopatry.

We used the global model $\Phi(g*t)\ p(g*t)$ for testing bootstrap GOF, where 'g' is the sex of juvenile, and 't' is time (monthly).

We tested whether group size influence dispersal pattern of offspring by grouping them into two categories; (L) offspring in large groups ($\geq$ 5 birds) (n = 22), and (S) for offspring in small groups (2-4 birds) (n =13). We tested GOF with parametric bootstrap procedure of the global model $\Phi(g*n*t)\ p(g*n*t)$ where 'n' represents group size.

We evaluated whether the presence/absence of helper(s) influenced natal dispersal or the probability of remaining in the natal territory. Offspring in groups of a breeding pair with no additional adults were grouped as 'Nh' (no helper; n = 20), and offspring in groups with at least one helper were labelled 'H' (n =15). We initiated the model with both sexes combined to examine how the presence/absence of helper(s) contributed to the model likelihood. Then we added sex 'g' into the models. We used the global model $\Phi(g*h*t)\ p(g*h*t)$ for testing bootstrap GOF where 'h' represents presence/absence of helper(s).

4.2) Juvenile dispersal

Fledglings of known family groups were monitored for weekly survival until independence from nutritional parental care (eight weeks post fledging). During each monitoring event, we searched throughout the natal territory for up to two hours to monitor number of young that reach to age of independence. Our results report on findings for 41 juveniles (18 females, 17 males, and six of unknown sex). This represents 61% of all fledglings from both years, while the other 39% did not survive to independence (Sankamethawee et al. 2009). We conducted weekly surveys for fledged birds in each natal territory until the end of the breeding season (July). During the non-breeding season (August-January), we monitored each territory once every two weeks at minimum. Resighting histories for birds were recorded as 1 for observed and 0 for not seen during each monitoring session.

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4.3) Dispersal distance

We searched for dispersing birds via three different methods 1) searching within the study population (as described above), 2) randomized area searches in the extended plot, and 3) random walks outside the extended plot area within a 3-km radius of the 30 ha MST plot. First, we searched all neighbouring territories adjacent to the juvenile natal territories for the presence of new group members. We were explicitly searching for young birds with known identities that may have dispersed to neighbouring territories outside the core study population. Second, the study area was extended 400 m in four

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directions (North, East, West, and South) outside the 30 ha MST plot. We conducted randomized area searches for at least 25 % of each side of the extended areas during six surveys; two during the 2007 breeding season; two during the 2007 non-breeding season; and two during the 2008 breeding season. Two observers were used on each survey to improve detection rates and to facilitate following of any groups encountered in order to identify ringed birds. A total of 192 observer-hours were spent covering the 132 ha area. Third, we walked the trail system to intensively search for dispersing birds beyond the extended plot during the first week of May until 17 August 2008, for at least 120 hours (approximately one to two days per week). We used eight major walking tracks (totalling ca. 58 km) within an approximately three km radius from the plot to search for dispersing birds. Any calling or visually detected Puff-throated Bulbuls was followed until it was identified as ringed or unringed or we lost track of that individual.

We define natal dispersal as permanent movement away from the natal territory to a new settlement area, whether directly to a breeding vacancy (Greenwood 1980) or to a new territory where individuals do not breed but are in a 'staging post position' (Cockburn et al. 2003). However, we confirmed dispersal for those birds that were resighted in the same area one month or more after the first detection. Territory mapping was not possible for those birds dispersed outside the 30 ha plot, because most birds except the dispersing ones were unringed, thus we were unable to determine the centre of the new territories. We measured the straight line distance from hatching site to the first sighting at the new territory and estimated dispersal distance as the number of territories crossed from natal territory to the new territory (sensu Daniels and Walters 2000, Cockburn et al. 2003, Eikenaar et al. 2008). Dispersing to a neighbouring territory resulted in crossing one territory (Daniels and Walters 2000), and the birds remaining in their natal territory are defined as having a dispersal distance of zero. For birds that were not located and presumed to have dispersed further than the extended plot, we estimated the minimum possible dispersal distance based upon the shortest straight line distance to the nearest edge. While we realize this is likely an underestimate of actual distance moved, it is a useful guideline for understanding the minimum spatial extent of dispersal. We tested whether males and females disperse similar distances using Mann-Whitney U tests.

5. RESULTS

In no cases (n = 41) did juveniles disperse away from their natal territories during their hatching year. All offspring dispersed in their second calendar year prior to and during the first breeding season after

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they fledged. Five of 18 females (27.8 %) relocated to new territories. Two of these females settled in the study plot, while the other three dispersed outside the core study area (Table 41). Another 12 dispersing females (66.7 %) were never located and assumed to have dispersed outside the study tract or died while dispersing. One female remained with parents and was observed helping at a nest during the first breeding season. Ten of 20 males (50%) remained in natal territories as helpers, six (30%) dispersed to a known location, and four (20%) were not located post dispersal (Table 14).

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5.1) Dispersal distances

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For birds dispersing to known locations, dispersal was distinctly female biased; females dispersed 2.5 times or more farther than males. The mean dispersal distance (± SD) for females was 554 ± 267 m (range 311-980 m, n = 5), and 175 ± 84 m (range 83-322 m, *n* = 6) for males. The median territory size (± SD) of the MST population was 1.53 ± 0.5 ha (n = 30). Thus, the median diameter of territories was 142.5 m assuming territories were roughly circular. Females moved across 2-7 territories before settling, while five of six known fate dispersing males moved to adjacent territories or at a distance of one territory. Only one located male dispersed across two territories (Table 14, Figure 3). Dispersal distance when excluding philopatric birds shows that females (n = 5) dispersed significantly farther than males (n = 6) (Mann-Whitney U, Z = -2.556, P = 0.011). This pattern is even stronger when philopatric birds are included; male n = 16, and female n = 6 (Mann-Whitney U, Z = -2.837, P = 0.005).

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The average minimum dispersal distance of birds that are presumed to have dispersed off plot was 501 m (range 364-629 m) (N=20). When separated by sex, the mean minimum dispersal distances were similar: 495 m for females (range 412 - 629 m), and 509 m (range 364 – 605 m) for males. When combined with the known settlement individuals (known locations n = 13, unknown locations n = 20, and philopatric offspring n = 11) the mean dispersal distance for all individuals was 325 m (range 0-980 m). As the study area is a large continuous primary forest patch, we presumed similar densities and territory sizes of birds in and off the study plot. The mean dispersal distance (± SD) for all females was 483 ± 188 m (n = 18), crossing 3.4 ± 1.3 territories, and for all males was 154 ± 207 m (n = 20), crossing 1.0 ± 1.5 territories (Mann-Whitney U, Z = -3.7, P < 0.001).

5.2) Probability of staying

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The best fitting models for all interaction groups strongly supported a breeding season effect on dispersal. This indicates that the probability of staying in the natal territory is constant during the first non-breeding season after hatching (nbr(.) (model 1; Table 2~~5~~). Using a threshold of $\hat{C} < 3$, to suggest minimal overdispersion of the data (Lebreton 1992), all of the $\hat{C}$ values from GOF tests were < 2. These included 1.53 for the overall dataset (male + female), 1.39 for separated by sex, 1.54 for the helper dataset, and 1.42 for the group size dataset. Thus the models fit the data under the CJS model assumptions, and these $\hat{C}$ values were used to adjust for minor levels of overdispersion.

The probability of resighting or detecting remained constant over time (models 1 and 2; Table 2~~5~~). The breeding interval model (model 1; Table 2~~5~~) was > 29,000 times, and > 30,000 times more likely supported than the null model and the global model (models 4 and 5; Table 2), respectively. The cumulative survival probability in the natal territory (probability of staying) suddenly decreased at the beginning of the first breeding season (January-February) post fledging and then gradually decreased until the end of the breeding season (July) (Figure ~~2~~4a). The probability of staying in the natal territory at the end of the breeding season after the hatching year was 0.30 ± 0.07 SE for both sexes combined.

Sex had a clear effect on philopatry and dispersal (Figure ~~2~~4a). The most parsimonious survival models of sex-dependent effects (models 6 and 7; Table 5) demonstrate that the probabilities of surviving during the non-breeding season were similar for both sexes and constant over time, but largely different during the breeding season (Figure ~~2~~4a~~a~~) which contributed 100% to the QAIC$_c$ weights. The best-fitting model (model 6; Table 2~~5~~) was > 30,000 times more likely supported than the null and global models (models 9 and 10; Table 2~~5~~). Based on model averaging, the probability of staying in the natal territory until the end of their first breeding season for females was 0.09 ± 0.08 and 0.60 ± 0.04 for males.

Effects of group size on sex-related dispersal: The number of individuals in a group did not affect either the probability of dispersal or the probability of resighting (models 1- 4; Table 3~~6~~). The most parsimonious model incorporated group size (model 6; Table 3~~6~~) and was 19 times less likely supported than the best-fitting model of breeding season and sex effects (model 1; Table 3~~6~~), while the best-fitting model was >35,000 times more likely supported than the global model (model 7; Table 3~~6~~). In general, the best-fitting models are supported by breeding season and sex effects.

Presence of helper(s)/co-breeders in a family group contributed to the probability of staying for males but not for females (Figure 4~~2~~b). The model suggesting males in groups without helpers had different dispersal rates than those with helpers showed 15% support based on the QAIC$_c$ weights (model 9; Table ~~6~~3). Hence, males in groups without helpers were more likely to remain in the natal territory than were males in groups with helpers. The best-fitting model of sex effects during the breeding season (model 8; Table ~~6~~3) was 5.4% more likely supported by the data than the best-fitting

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helper model (model 9; Table ~~6~~3). The probability of staying ‘home’ by the end of the first breeding season for males in groups with helper(s) was 0.45 ± 0.08 and for males in groups without helper(s) was 0.62 ± 0.04.

6. DISCUSSION

Our results support the finding that fledging survival is generally higher for individuals fledging early in the season (Krementz et al. 1989, Verboven and Visser 1998, Naef-Daenzer et al. 2001, Wheelwright et al. 2003), but see Tinbergen and Boerlijst (1990) and Magrath (1991). Some breeding pairs re-nest up to seven times in a single breeding season (Sankamethawee et al. 2010), and most adults spend time and energy on multiple nesting attempts due to high rates of nest predation (Pierce and Pobprasert 2007). If effort towards re-nesting potentially reduces breeding performance of adult birds as the breeding season progresses (Monrós et al. 2002), it is not surprising that young produced later in the breeding season may exhibit poorer fledgling condition and hence, reduced survivorship.

ที่จัดรูปแบบ: เต็มแนว

One limitation of this study was the relatively small number of fledglings, despite finding >300 nests, due to characteristically high predation rates in the tropics (Stutchbury and Morton 2001). Also, the undulating terrain and tall canopy makes following birds challenging and may result in periodically missing juveniles during a particular week post-fledging. However, given the amount of time spent in the field (>370 observer-hours per month) during the breeding season, we are confident we followed birds through to off-plot dispersal or disappearance.

Our research provides insights to the breeding biology and factors influencing post-fledging survivorship of tropical birds, particularly cooperative breeding species in the little-studied Asian tropics. We observe small clutch sizes, low nesting success, extended parental care, high juvenile and adult survival in Puff-throated Bulbuls, consistent with reported traits of other passerines in the tropics/southern hemisphere. Some life history aspects of this species are still unanswered such as territory turnover rate and lifetime reproductive success which is likely correlated with adult survival, prolonged parental care and juvenile dispersal and data concerning nearly all other sympatric species are completely unknown. Thus, long-term studies of the same population with comparisons to other sympatric bulbuls would be particularly informative for understanding life-history tradeoffs in tropical passerines.

Puff-throated Bulbuls engage in all three main characteristics of cooperative breeding (Brown 1987). First, all offspring delayed dispersal and remained with parents for a long period (up to 12 months) despite being nutritionally independent from parental care at the age of two months. Second, all philopatric males delayed breeding, although some dispersing individuals attempted to breed. Third, offspring of both sexes acted as helpers, as has been otherwise shown (e.g. Curry and Grant 1990, Doerr and Doerr 2006, Cockburn et al. 2003). Here we explore these three strategies in Puff-throated Bulbuls in relation to relevant hypotheses on cooperative breeding.

ที่จัดรูปแบบ: เต็มแนว

Puff-throated Bulbuls remain with their parents for a minimum of six months after fledging, indicating a long period of parental investment. This prolonged investment of parents during the first year of life can be explained by nepotism (Kokko and Ekman 2002, Griesser 2003) that favours philopatry (Ekman et al. 2000). Association of retained offspring with their parents and within the natal site in sedentary species is often associated with delayed dispersal (Brown 1987, Ekman et al. 2004), as we observe in Puff-throated Bulbuls. Adults are thought to control this strategy by promoting increased juvenile direct fitness via access to resources (Ekman and Griesser 2002, Covas and Griesser 2007). Furthermore, foraging in groups not only promotes kin selection but may help juveniles to improve their foraging skills, increase territory defence, and aid in predator recognition (Griesser 2003, Griesser and Ekman 2004). Juveniles of both sexes may increase the family fitness by remaining with parents if remaining results in increased probability of survival to sexual maturity. Remaining in family groups as observed in Puff-throated Bulbuls is consistent with the benefits of nepotism hypothesis in which survivorship during the independent but less experienced period during the first year post-fledging is relatively high.

In their first year after fledging, male Puff-throated Bulbuls either stay home as helpers, disperse to neighbouring territories (either as breeders or as non-breeding helpers), or float and are difficult to detect. Philopatry is the preferred option for young males (Miller and Smallwood 1997, Pasinelli and Walters 2002, Cockburn et al. 2008), who tend to queue for breeding vacancies both in their natal and neighbouring territories (Cockburn et al. 2003), as we observe in our study system. The philopatry advantage hypothesis explains that helpers can gain both direct and inclusive fitness (e.g. Covas and Griesser 2007, Cockburn et al. 2008) and it has been shown that survivorship of philopatric males is higher than those who disperse (Rowley and Russell 1997). In addition, delayed breeding males exhibit higher lifetime reproductive success than males who start breeding at a younger age (Ekman et al. 1999). If consistent with findings in other studies, male Puff-throated Bulbuls in groups with no helpers may experience higher survival than those dispersed from groups with helpers because they are more likely to remain philopatric. Our observations suggest that philopatric males help by mate-guarding the breeding female during nest building, feeding nestlings and fledglings, engaging in anti-predator behaviour and defending the territory. Philopatric behaviour would result both in increasing inclusive fitness and also increase their own breeding skills (Craffey 1992). Also, familiarity with neighbours may increase the efficiency of vacancy prospecting, which can increase success at filling breeding vacancies when they occur (Eikenaar et al. 2008).

No philopatric males attempted to breed (as primary territory holders) during their first year post fledging, in spite of being sexually mature. In contrast, at least three of six (50%) of dispersing males attempted to breed, though none bred successfully during their first year post-dispersal. The cost of maintaining and defending a new territory independently may be high (Covas and Griesser 2007), particularly when less-experienced birds face less familiar surroundings, new neighbours, and predators. ‘Staying home’ could be the better option to optimize future breeding opportunities (Kokko and Johnstone 1999) and maximize lifetime reproductive success (Ekman et al. 1999). At our study site, the youngest male to breed successfully was three years old. This male mated with the most successful female known in our study, who produced ten young during the last four breeding seasons.

Natal dispersal of Puff-throated Bulbuls is female-biased and occurs via direct dispersal to a breeding vacancy, dispersal to a staging post as non-breeder in a foreign territory, remaining a as helper for a short period of time and dispersing later in the first breeding season, or remaining in the natal territory as a helper throughout the breeding season. The first two options are the most frequent (83.3 % of cases), the third occurred in two cases, and the fourth occurred only one. Female-biased dispersal in Puff-throated Bulbuls is clear both in frequently and distances (Table 1), which is typical for most birds (e.g. Greenwood 1980, Miller and Smallwood 1997, Woxvold et al. 2006). Unlike dispersing males who frequently occupy neighbouring territories, females in our system never dispersed to neighbouring territories. Females of other cooperative breeding species move to neighbouring groups as a staging post (Cockburn et al. 2008, Eikenaar et al. 2008) or acquire breeding status in neighbouring territories (Curry and Grant 1990, Yáber and Rabenold 2002), which is not something we observe in our system.

For females, dispersing confers an advantage when the cost of group conflict and inbreeding pressure is greater than breeding away from close relatives. For example, young female superb fairy-wrens “choose” not to breed in their natal territory, even when vacancies are available (Cockburn et al. 2003). Also, females are presumed to be more selective with respect to sexual partners than are males (Cockburn 2004), thus dispersing is a good means of seeking a prospective mate within a high quality territory. In two cases females helped parents to feed nestlings of early broods before dispersing. Perhaps this experience results in increased reproductive success later in life. While we do not yet have data to support this idea, it merits further study. Furthermore, female helping regardless of territory inheritance can probably be explained by a strong kin structure associated with inclusive fitness in Puff-throated Bulbuls, though this advantage remains unclear for immigrant helpers or those from unknown origins.

Dispersal of young Puff-throated Bulbuls was strongly associated with the commencement of the breeding season in the second year. Territory occupancy appears particularly important, as inexperienced males disperse when space becomes available. For example, two male birds that acted as helpers quickly filled breeding vacancies in neighbouring territories within one week of adjacent male breeders disappearing. Another second-year male remained and helped parents to rear offspring before moving to breed with a widowed female when a breeding vacancy occurred at the end of the same first breeding season. Another male dispersed to a neighbouring territory as a helper in his second year before moving to a vacancy when a breeding male disappeared from a neighbouring group. After becoming a breeder, this male was observed to interact with his mother's group and the neighbouring group regularly. Interestingly, while he was a breeder, he was observed to help another female in an adjacent territory by feeding young at her nest. While we do not know if he sired those offspring, such questions are also worth further investigation.

ที่จัดรูปแบบ: อังกฤษ (สหรัฐอเมริกา)

Our results suggest that group size did not influence dispersal decisions of either males or females. For females this may be linked to dispersing away from the natal territory to avoid inbreeding, but the benefit is less clear for the males. In our system breeding vacancies appear to be limiting (see above), and thus group size may be less important than queuing as helper. In stable social groups, older birds or older helpers are competitively superior over subordinates (Cockburn et al. 2008) and they may have an increased probability of 'winning' sites as vacancies occur (Pasinelli and Walters 2002, Cockburn et al. 2003, 2008). Thus breeding vacancy and queuing may relate to the presence of helpers. The costs of queuing in a group with dominant helpers might be outweighed by lifetime reproductive benefits, particularly in long-lived tropical species with relatively slow territory turnover rates. However, our results showed only 15% support relative to all other models in the candidate set. Thus for some philopatric males in groups with older helpers, queuing may be for access to vacancies on neighbouring territories (Kokko and Ekman 2002, Cockburn et al. 2008). We observed at least one male remaining as a helper in the same group for a minimum of four years (2005-2008), which suggests a low breeding vacancy rate and begs the question of the advantage of queuing as a subordinate in our system.

Although dispersal has long been investigated in conjunction with both social and ecological factors, it is still challenging to understand the myriad social effects that influence timing and distance of dispersal for cooperative breeding species. We found clear differences between sexes, both with respect to timing and distance of dispersal. In our system, group size and co-breeding varies widely, as does both presence and number of helpers. A longer-term study can provide a clearer picture of how dispersal patterns may change through time, particularly as lifetime reproductive success and reproductive queuing stability are further explored. Our results broaden our understanding of how dispersal patterns of offspring reflect the kin structure in cooperative breeding birds from a little studied lineage and region. The wide array of strategies that co-exist in space and time points to the complexities of teasing apart drivers of cooperative breeding and substantiates that a number of hypotheses likely contribute to the patterns we observe.

Radio telemetry –using radio telemetry on small size passerines to study natal dispersal is not an appropriated method, particularly if those birds are natal philopatric as we found in this study. However, it can be a useful tool to study pre-dispersal movement while those birds stay with their family group. However, by doing that, the radio should be tagged in nestling before they leave the nest. Thus, collecting data on their movement can be done only the first 2 months after they leave the nest, which is not close to the dispersal time. The other problem is that the probability to capture the juvenile birds prior dispersal is extremely difficult. Thus studying natal dispersal in small cooperatively breeding birds is very expensive and time consuming.

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ที่จัดรูปแบบ: อังกฤษ (สหรัฐอเมริกา)

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ACKNOWLEDGEMENTS

We thank to J. Khoonwongsa for her assistance with fieldwork. We thank A. J. Pierce and P.D. Round for supervision and collaboration in bird ringing. We thank all who supplied additional field data especially N. Sukumal, D. Khamcha, S. Tanasarnpaiboon, and K. Pobprasert. We thank P. Wonkson for conducting DNA sexing at KMUTT, B. D. Hardesty and S. Metcalfe at the tropical forest research centre, CSIRO, Australia for helping with DNA sexing. We thank the Department of National Parks, Wildlife and Plant Conservation for permission to conduct research and the Khao Yai training centre for accommodation. Research funding was provided by the KMUTT research grant fiscal year 2008-2009.

8. PROJECT OUTPUTS

Lectures, workshops and conferences

1) Oral presentation in CSIRO internal seminar 27 November 2008, at the Tropical Forest Research Centre, Atherton, Queensland, Australia.

2) Oral presentation in “33rd Annual Conference of the Ecological Society of Australia : Interactions in Science, Interactions in Nature” at University of Sydney , Australia.

3) The project presented posters at 2nd International Field Ecology Symposium: Ecosystems Management and Conservation. Bangkok: 25-28 January 2007, King Mongkut's University of Technology Thonburi.

4) Oral presentation in การประชุมวิชาการประจำปีโครงการ BRT ครั้งที่ 12 ระหว่างวันที่ 10-13 ตุลาคม 2551 ไดมอนด์พลาซ่า จ.สุราษฎร์ธานี

5) ฝึกอบรมนักศึกษาฝึกงานจากคณะสัตวแพทยศาสตร์ จุฬาลงกรณ์มหาวิทยาลัย และมหาวิทยาลัยขอนแก่น ในช่วงภาคการศึกษาฤดูร้อน ~~2550 และ 2551~~ ในการใช้และติดตามการเคลื่อนที่ของนกโดยวิธี radio telemetry และเทคนิคการจับนก เพื่อทำเครื่องหมายประจำตัว รวมทั้งการศึกษาวิจัยในแปลงถาวรมอสิงโตในภาพรวม

6) วิทยากรฝึกอบรมการดูนกและศึกษาวิจัยเกี่ยวกับนกให้กับผู้เข้าร่วมอบรมประจำปีของศูนย์ฝึกอบรมป่าไม้ที่ 2 (เขาใหญ่) ทั้งหมด 3 ครั้ง

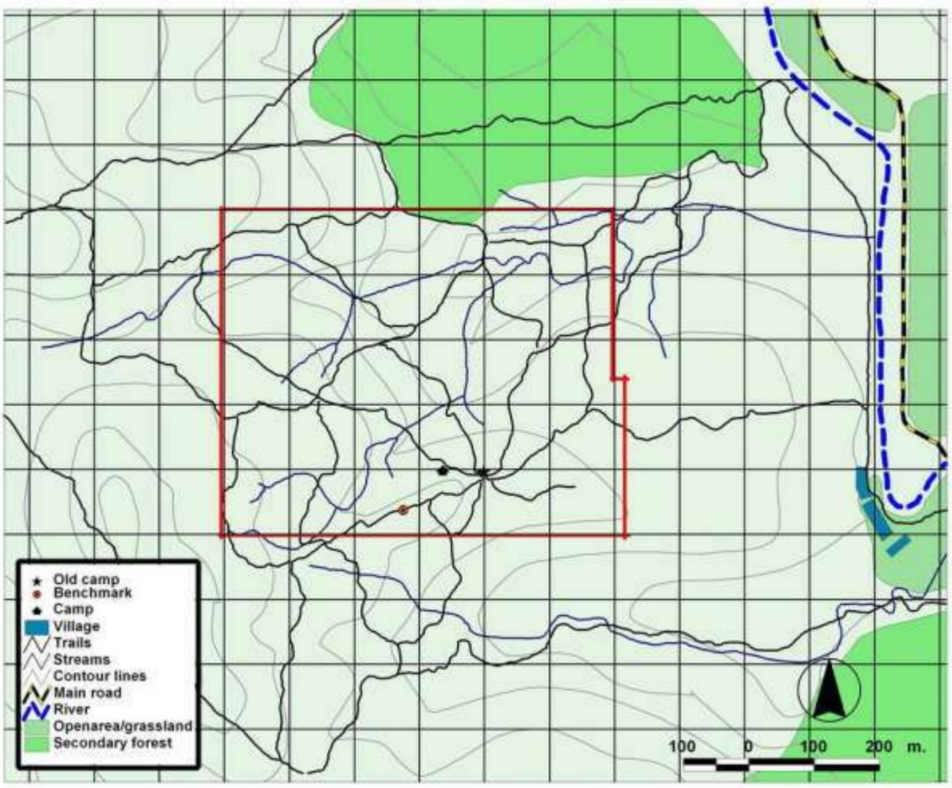

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Figure 1. Map showing the location of the Mo-Singto Long-term Biodiversity Plot near the headquarters of Khao Yai National Park.

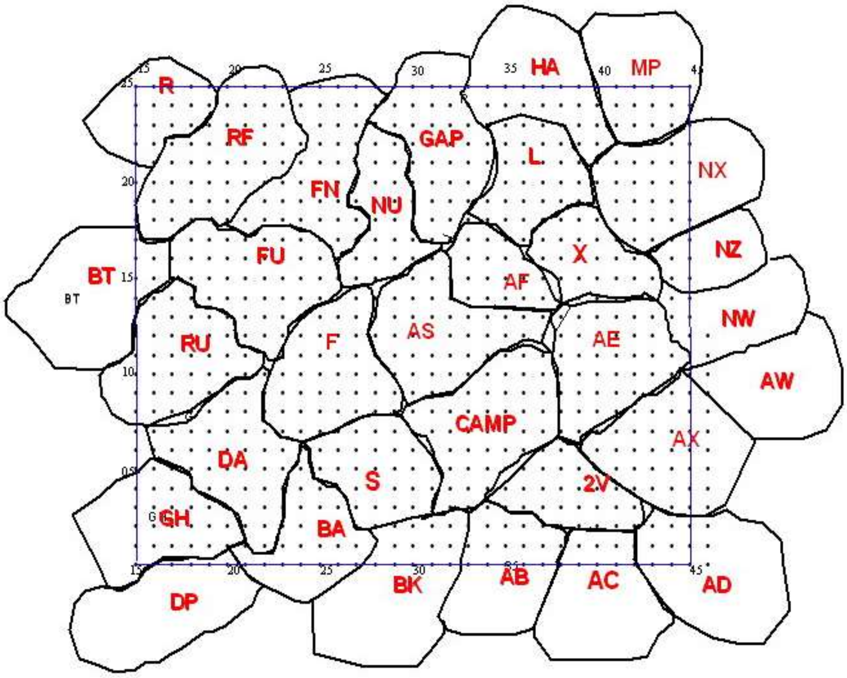

Figure 2. Map showing the territories of Puff-throated Bulbuls occupying the Mo Singto plot area during 2006-2008.

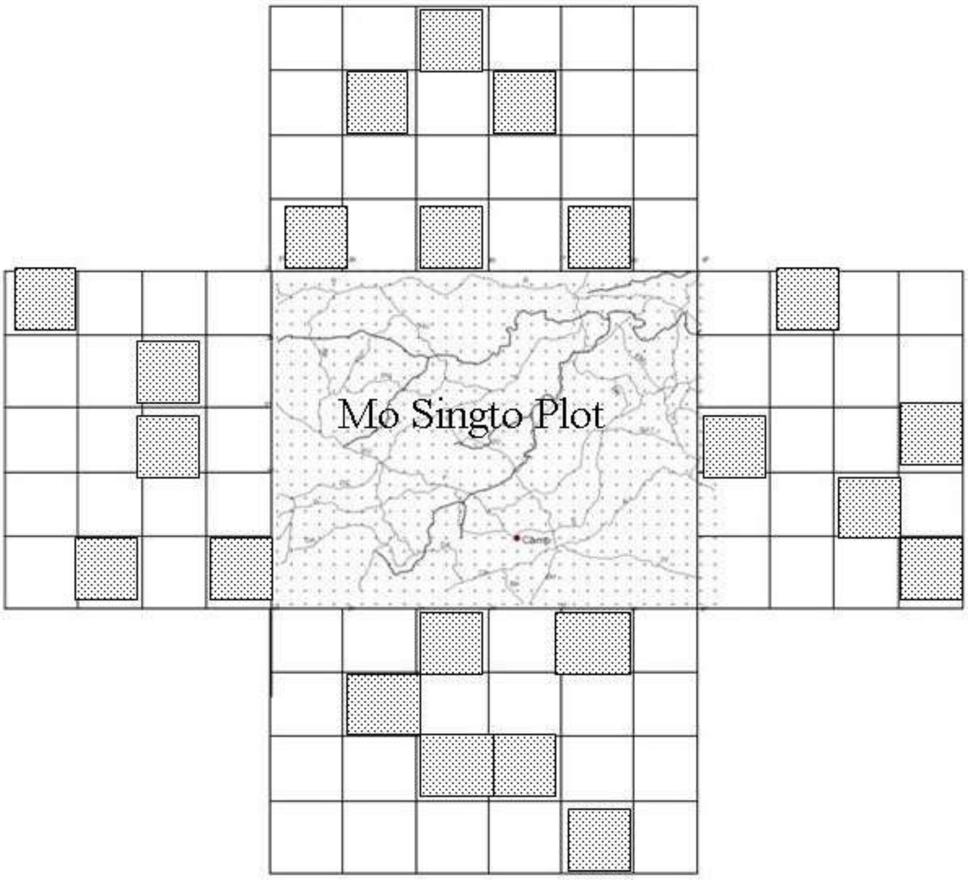

Figure 3. Map showing one survey occasion for randomized area searches outside the Mo Singto plot. Dotted squares show a twenty-five percent of each side of the extended plot.

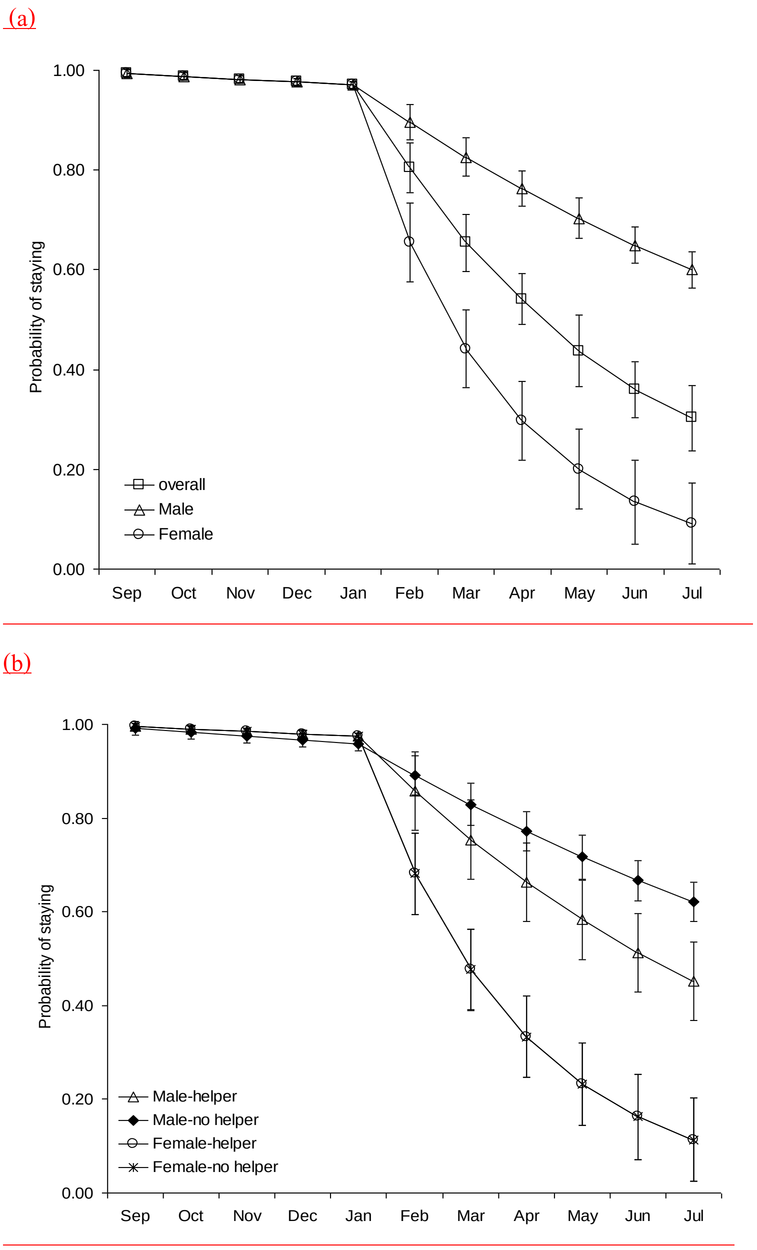

Figure 4. Probability of staying (cumulative survival probability (± SE) in natal territory of offspring Puff-throated Bulbuls. Part (a) Demonstrates the overall and sex-dependent patterns, (b) demonstrates the effects of the presence/absence of helpers. Five monthly intervals from August to

January represent the non-breeding season when juveniles are independent from nutritional parental care, and 6 monthly intervals from January to July represent the breeding season after hatching year.

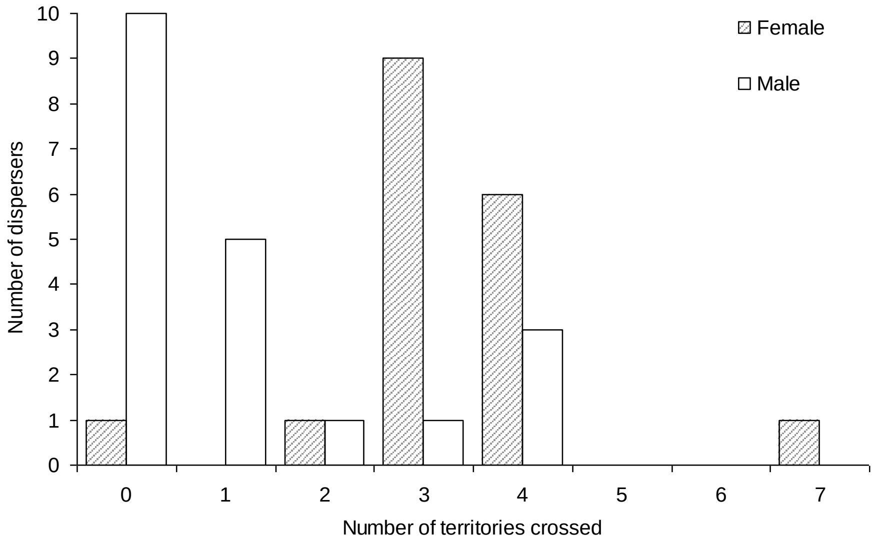

Figure 5. Frequency of natal dispersal distances of known sex offspring Puff-throated Bulbuls (18 females and 20 males) including known dispersal locations (n = 11), natal philopatric (n =11), and individuals never relocated, estimated from the minimum possible dispersal distance (n =16). The number of territories crossed estimated from the median territory diameter 142.5 m.

Table 1. Summary of dispersal patterns of offspring Puff-throated Bulbuls. Numbers in parentheses of known dispersal locations indicate confirmed breeder status. Dispersal distance estimated as number of territories crossed based on the median territory diameter of 142.5 m. [a] Known dispersal location individuals, [b] all individuals including philopatric birds (n = 11), located birds (n = 13), and birds never located estimated from minimum dispersal distances (n =20).

Dispersal patterns	Female	Male	Unk. sex
Philopatric	1	10	0
Known dispersal location	5(2)	6(3)	2
Unknown dispersal location	13	4	4
Dispersal distance range measured as number of territories crossed (excluding philopatric birds)	2-7	1-2	1
Mediam dispersal distance ± interquartile range (m)	554±267	175 ± 84	154
Median number of territories crossed (excluding philopatric birds) ± interquartile range	3.9 ± 1.9	1.2 ± 0.6	
Mean territories crossed (including birds never located)	3.4 ± 1.3	1.0 ± 1.5	2.7 ± 1.4
Cumulative probability of staying in natal territory ± SE	0.05 ± 0.04	0.58 ± 0.14	-

Table 2. Mark-resighting models to determine (A) timing and (B) sex-dependent effects on natal dispersal of Puff-throated Bulbuls. QAIC$_c$ for overall dataset (a) adjusted for $\hat{c}$ = 1.53 (n = 35), and sex effect (b) adjusted for $\hat{c}$ = 1.39 (females n = 18; males n= 17), nbr = non-breeding season (5-month intervals from August to January), br = breeding season (6-monthintervals from January to July), (.) no effect or constant, g = sex, and t = time (monthly).

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ Weights	*K*
(A) overall (male + female)				
1. Φ(nbr(.), br(.) *p*(nbr(.), br(.)	173.35	0.00	0.88	4
2. Φ(nbr(.), br(t) *p*(nbr(.), br(.)	177.89	4.54	0.09	9
3. Φ(nbr(.), br(.) *p*(nbr(.), br(t)	180.73	7.39	0.02	9
4. Φ(.) *p*(.)	193.98	20.64	0.00	2
5. Φ(t) *p*(t)	198.99	25.65	0.00	22
(B) sex				
6. Φ(nbr(.), br(g) *p*(nbr(.), br(g)	180.30	0.00	0.63	6
7. Φ(nbr(.), br(g) *p*(nbr(g), br(g)	181.38	1.08	0.37	7
8. Φ(nbr(.), br(g*t) *p*(nbr(g), br(g)	190.97	10.66	0.00	17
9. Φ (.) *p*(.)	213.12	32.81	0.00	2
10. Φ(g*t) *p*(g*t)	247.15	66.85	0.00	44

ที่จัดรูปแบบ: ฝรั่งเศส (ฝรั่งเศส)

ที่จัดรูปแบบ: ฝรั่งเศส (ฝรั่งเศส)

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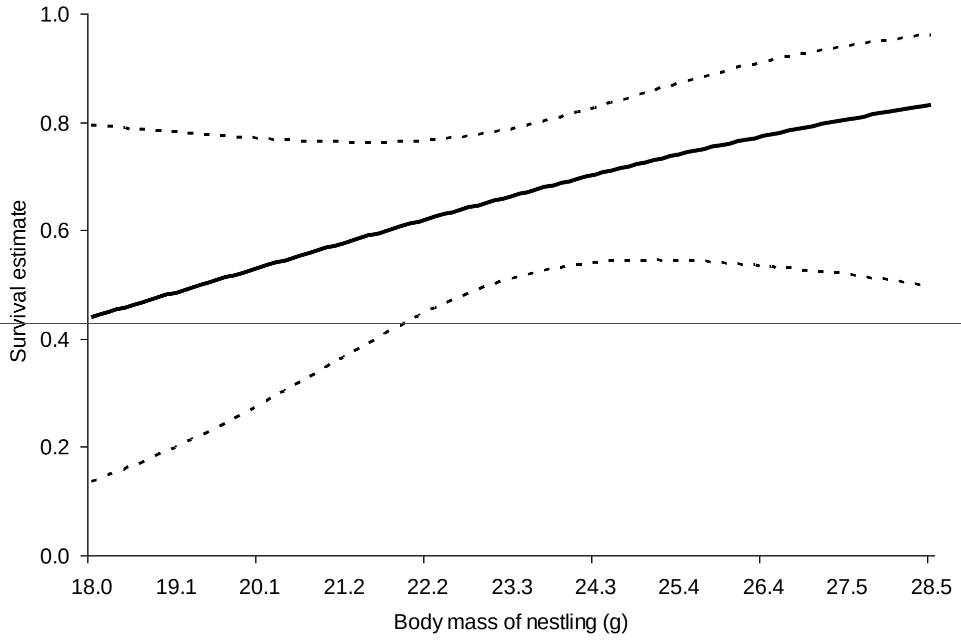
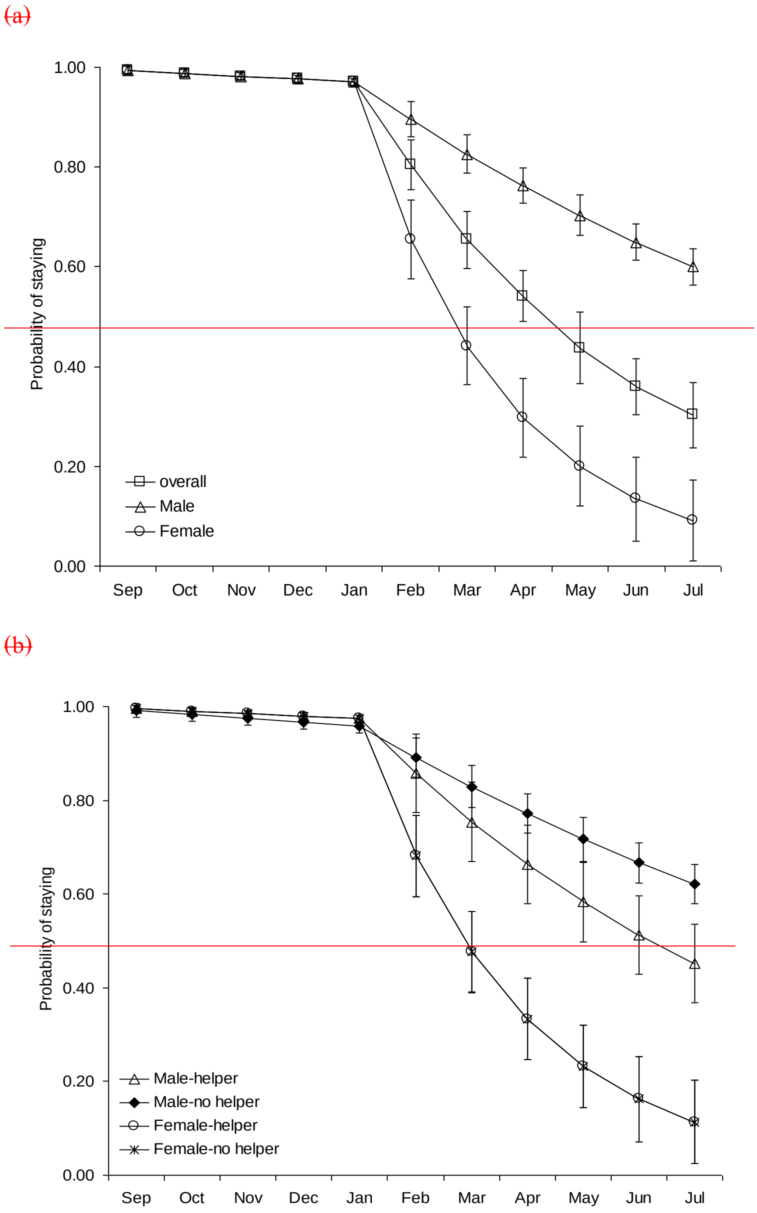
ที่จัดรูปแบบ: ฝรั่งเศส (ฝรั่งเศส)

Table 3. Mark-resighting models to determine the effects social factors; (a) sex and group size, and (b) sex and helpers on natal dispersal patterns of Puff-throated Bulbuls. QAICc for group size dataset (a) adjusted for $\hat{c}$ = 1.53 (large groups n = 22, small groups n= 13), helper dataset (b) adjusted for $\hat{c}$ = 1.54 (groups with helper(s) n = 15, groups without helper(s) n= 20), nbr = non-breeding season (5 intervals August to January), br = breeding season (6 intervals January to July), (.) no effect or constant, g = sex, n = group size, h = presence/absence of helpers, M-Nh(uniq) = males in groups with no helper(s). These were treated as a unique parameter, while all females and males in groups with helper(s) were similar and treated as constant, and t = time (monthly).

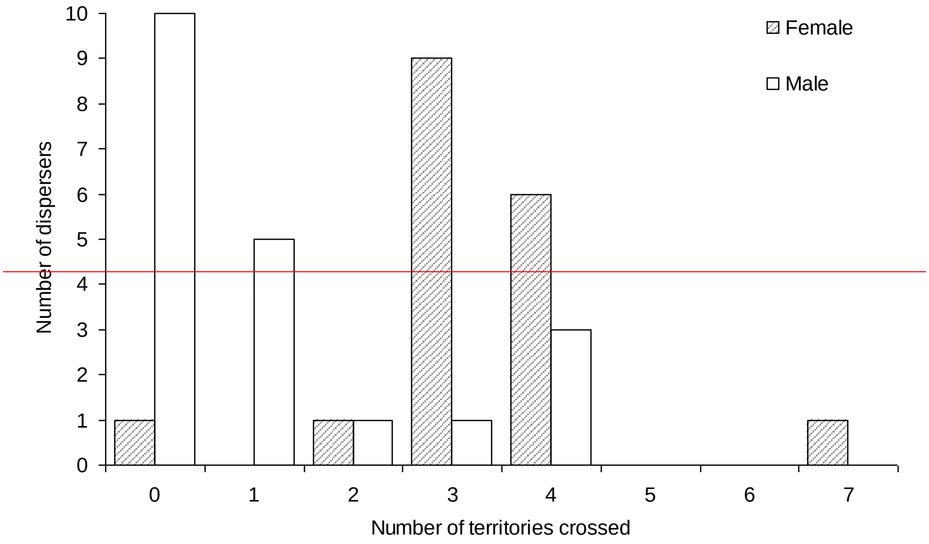
Model	QAIC_c	$\Delta\mathrm{QAIC}_c$	QAIC_c Weights	K
(A) sex & group size				
1. Φ(nbr(.),br(.) p(nbr(g),br(g)	184.97	0.00	0.41	6
2. Φ(nbr(g),br(g) p(nbr(g),br(g)	187.52	2.55	0.11	8
3. Φ(nbr(g),br(g) p(g)	187.74	2.77	0.10	6
4. Φ(nbr(.),br(g*t) p(g)	187.90	2.92	0.10	15
5. Φ(nbr(g),br(g) p(.)	189.61	4.64	0.04	8
6. Φ(nbr(.),br(t) p(g*n)	190.85	5.88	0.02	11
7. Φ(g*n*t) p(g*n*t)	367.86	182.89	0.00	84
(B) sex & presence of helper(s)				
8. Φ(nbr(.),br(g) p(M-Nh(uniq)	166.53	0.00	0.83	5.00
9. Φ(nbr(.),br(M-Nh(uniq) p(M-Nh(uniq)	169.90	3.37	0.15	4.00
10. Φ(.) p(.)	192.75	26.22	0.00	2.00
11. Φ(g*h*t) p(g*h*t)	352.10	185.56	0.00	84.00



~~Figure 1. Predicted survival probabilities (± 95% CI) during the first week post-fledging of Puff-throated Bulbuls with different nestling body masses. Nestlings were weighed 2-3 days prior to fledging.~~



~~Figure 2. Probability of staying (cumulative survival probability (± SE) in natal territory of offspring Puff-throated Bulbuls. Part (a) Demonstrates the overall and sex-dependent patterns, (b) demonstrates the effects of the presence/absence of helpers. Five monthly intervals from August to January represent the non-breeding season when juveniles are independent from nutritional parental care, and 6 monthly intervals from January to July represent the breeding season after hatching year.~~



~~Figure 3. Frequency of natal dispersal distances of known sex offspring Puff-throated Bulbuls (18 females and 20 males) including known dispersal locations (n = 11), natal philopatric (n =11), and individuals never relocated, estimated from the minimum possible dispersal distance (n =16). The number of territories crossed estimated from the median territory diameter 142.5 m.~~