รายงานฉบับสมบูรณ์

โครงการวิทยานิพนธ์

Post-fledging survival and juvenile dispersal of a cooperatively breeding Puff-throated Bulbul (*Alophoixus pallidus*)

(BRT_T350006)

(1 มีนาคม 2550 – 28 กุมภาพันธ์ 2552)

เสนอ

โครงการพัฒนาองค์ความรู้และศึกษานโยบายการจัดการทรัพยากรชีวภาพแห่งประเทศไทย (BRT)

โดย

วังวร สังฆเมธาวี และ George A. Gale

Conservation Ecology Group

คณะทรัพยากรชีวภาพและเทคโนโลยี

มหาวิทยาลัยเทคโนโลยีพระจอมเกล้าธนบุรี

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%) 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. 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

Realistic estimates of juvenile survival are important for explaining fundamental life-history differences between tropical and temperate species and for understanding population dynamics of birds in general (Sandercock 2000). To date, most avian studies on survivorship have been conducted in temperate regions (Brouwer et al. 2006) while little is known about factors affecting survival and population sizes of tropical birds (Martin 1996). Information from temperate regions, however, is not necessarily appropriate for explaining population dynamics in tropics because environmental factors are generally less variable between seasons (Martin and Karr 1986), and life histories of tropical species are typically characterized by smaller clutch sizes, lower nesting success, extended parental care and higher adult survivorship (Martin 1996. Arnold and Owens 1998, Russell et al. 2004, Brouwer et al. 2006).

Immediately after leaving the nest, birds typically face the highest mortality risks of their lifecycle (Wheelwright et al. 2003) due to limited flying skills and the variety of hazards they may encounter in their naïve state during this dependent period when parents still care for their young (Suedkamp Wells et al. 2007). This is also one of the most difficult stages to assess survivorship because juveniles are typically difficult to follow (McGowan and Woolfenden 1990, Magrath 1991, Suedkamp Wells et al. 2007). This may be particularly true in closed-canopy tropical forests with a high degree of topographical variation and for non-ground dwelling species. Consequently, little is known about how post-fledging survival contributes to population dynamics overall and particularly in the tropics.

Several factors have the potential to impact juvenile survival. Annual variation has a great effect on avian survival in some ecosystems where weather conditions are inconsistent (e.g. Yackel Adam 2006); and seasonal patterns have been shown to influence juvenile mortality (Komdeur and Daan 2005). The limited available data on post-fledging survival suggests that body mass at fledging is also a significant determinant of post-fledging survival with heavier birds experiencing increased survival (Tinbergen and Boerlijst 1990, Magrath 1991). Also, studies have demonstrated that timing of fledging, such as early versus late in the breeding season, correlates with juvenile survivorship (Krementz et al. 1989, Verboven and Visser 1998, Naef-Daenzer et al. 2001).

Sex-biased offspring survival is likely to result in biased adult sex ratios and may have several ecological and evolutionary consequences (Promislow et al. 1992), although it has rarely been demonstrated in fledglings (but see Green and Cockburn 2001). Parental care is important for food provisioning, for learning foraging and predator avoidance skills, as well as for protection from predators and the elements (Martin 1996, Griesser 2003). This may be amplified by helpers/or allo-feeders in cooperative breeding species (McGowan and Woolfenden 1989, Caffrey 2000, Doerr and Doerr 2006).

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).

The selective advantage of cooperative breeding in birds has long been a topic of interest in evolutionary biology. Such breeding and social systems are relatively rare; merely 3.2% of all avian species (Arnold and Owens 1998) are cooperative breeders.
Cooperative breeding in birds occurs when more than two birds care for offspring in the same nest or when individuals care for conspecific offspring that are not their own (Cockburn 1998, Arnold and Owen 1999, Doerr and Doerr 2006). Cooperative breeding species tend to experience low breeding rates, high adult survival, limited juvenile dispersal, and deferred maturity (Russell et al. 2004, Doerr and Doerr 2006).

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, Covas et al. 2006). 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. submitted). 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 how social status influence juvenile dispersal of Puff-throated Bulbul *Alophoixus pallidus*) in space and time.
2. To investigate how social status influence the settlement patterns of dispersing Puff-throated Bulbuls.
3. To investigate how juvenile survival during the first year influences population and social structure of

   Puff-throated Bulbuls in the subsequent year.
4. To obtain a better understanding of the role of an important forest seed-disperser.

3. METHODOLOGY

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 (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.

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.

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

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.

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 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.

4. DATA ANALYSIS

4.1) Post-fledging survival

Identification of helpers is based upon a number of cues. Adults that are present but not nesting separately within a group or territory are defined as helpers when they contribute to nestling and fledgling care. Such behaviour is verified through direct observation during nesting and fledging stages. In territories with plural breeders, birds may help the other pair if their own nests fail. We also defined these birds as helpers in such cases. In the absence of DNA fingerprinting by which to identify actual parents of offspring, we assume parents based upon behaviour of males around females that are known to be responsible for a given nest and/or offspring.

Only females contribute to nest building, incubating, and brooding of young, while males guard their females at all times. Females build open cup-shaped nests, generally in the understory (0.5-6 m high), although a small proportion (<5%) of nests are built >15 m above ground (Pierce et al. 2007). Most females attempt a second brood while the young from their first brood are 3-5 weeks out of the nest. Breeding males and helpers join the female in provisioning the young both during nestling and fledgling stages. All adults in the group share territory defending, alarm calling and predator mobbing and hence are considered helpers if they are not the presumed parents of fledglings. Groups move widely between understory and subcanopy layers during foraging.

We monitored Puff-throated Bulbuls occupying territories within and adjacent to the 30 ha permanent plot continuously from 2006-2008. Each territory was monitored at least weekly throughout the breeding season (February-July), and monthly in the non-breeding season (August-January). We walked exhaustively the entire 30 ha study area once per week to ensure no new groups or breeding birds were missed. Twenty–eight groups were present and monitored in 2006, 31 groups in 2007, and 32 groups in 2008.

Puff-throated Bulbuls on the Mo-Singto plot have been ringed and regularly surveyed for abundance since 2003, though not all individuals are ringed. We ring captured birds with a unique color combination of two colors and one Royal Thai Forest Department aluminum ring with a unique identifying number. We followed and identified individuals using binoculars starting at the beginning of the 2006 breeding season to record their foraging locations and encounters with other groups. We mapped encounter locations as territory boundaries (e.g. Woolfenden and Fitzpatrick 1984, Carmen 2004). We recorded the number of individuals and unique color ring combinations detected at each encounter event to determine group size. We considered individual birds as part of a group after detections/resightings were consistent for more than two months.

We searched for active nests of all breeding individuals throughout the entire breeding season (February-July) during each year of the study (minimum monthly effort = 370 observer hours) (n = 98, 152, and 74 nests in 2006, 2007, and 2008 respectively). We monitored all known breeding females at least once per week to determine their nesting stage (e.g. building, laying, incubating, and nestling) and we located a majority of all active nests and a minimum of 95% of all successful nests (those fledgling at least 1 young) each breeding season. We checked active nests regularly (every 2-3 days during the egg stage; every 3 days in the nestling stage) until failure or fledging. We ringed and weighed nestlings 8-9 days old (2-3 days before fledging). During nestling stages we observed feeding activity at the nests to determine whether adults which were not presumed parents were helping to provision. During three years of the study, eight nests fledged young from heights that were inaccessible for ringing chicks, and nine nests were found post-fledging.

Fledging date was defined as day 0 for survival history. After day 0, we monitored fledglings once per week until the end of week eight. Each week, we searched for fledglings of each group for up to two hours per group by searching throughout the entire territory. We recorded resighting histories for birds as 1 for observed and 0 for not seen. During our monitoring, we recorded if the fledglings were fed by adults to confirm helping behaviour by extra adults. Although fledglings started to feed partly independently at 3-4 weeks, they are fed by adults until weeks 7-8. After eight weeks, juveniles are assumed to be feeding independently, even if juveniles remain with adult groups within the parental territory.

Juvenile Puff-throated Bulbuls are visually distinguishable from adults in several ways. When feathers are fully-expanded (week four post-fledging), juveniles are distinguished from adults by bill color and the contrast of new and old wing feathers. The bill colour of juveniles is pale yellow, while grayish in adults. Adult plumage is typically uniformly olive-brown. In contrast, juveniles begin to molt at approximately four weeks so contrast between the olive new feathers and the brown old feathers is apparent.

Because male and female Puff-throated Bulbuls are visually indistinguishable, sexing in the field is not possible. Therefore, for captured birds and ringed nestlings, we collected approximately 10-15 μl of blood from the tarsus vein or brachial vein. Blood was stored in 1 ml lysis buffer for DNA extraction and subsequent polymerase chain reaction and analysis to determine sex.

Model development

We estimated weekly survival probabilities using program MARK (5.1) to fit Cormack-Jolly-Seber models (following Cooch and White 2008) to generate maximum-likelihood estimates of survival probabilities. We constructed capture-resighting histories of all fledglings (n = 87) for which nests were found prior to fledging; there were 23 fledglings in 2006, 37 in 2007, and 27 in 2008. To avoid violating the model assumptions regarding independence, we tested the effect of brood dependence by selecting only one randomly chosen individual from each brood (n = 41). Brood size was generally 2-3 individuals, thus single fledglings of more than 2-3 days old originating from unknown nests were excluded from the survival analysis to avoid broodmate biased survival estimates. Nine encounter histories (beginning week 0 through week 8) were analyzed for post-fledging survival.

Survival probability, Φ, is defined as the probability of a fledgling surviving from one week to the next, whether or not it was resighted. Resighting probability, p, is the probability that a bird will be resighted, given that it was alive. We checked goodness-of-fit (GOF) by simulation using parametric bootstrapping (1000 simulations) from the fully time dependent global model (t) for each dataset following Cooch and White (2008). The variance inflation factor ($\hat{c}$) was calculated as the observed deviance (global model deviance) divided by expected deviance simulated from parametric bootstrapping. Small sample corrected Akaike Information Criteria (AIC_c) values were adjusted to allow for the extent of overdispersion, measured by $\hat{c}$, to derive a quasi-likelihood ($QAIC_c$). The best-fit model is the one with the lowest $QAIC_c$ or $\Delta QAIC_c$ of zero (Lebreton et al. 1992), and models with a difference ($\Delta QAIC_c$) ≤ 2 are equally parsimonious to the best-fit model. We use $QAIC_c$ weights (w_i) to determine the relative likelihood of model fit against the set of candidate models.

First, we tested the age effect against the global or full-time dependent model Φ (t) p(t), by grouping time intervals (8 one-week intervals) into several categories. The time categories we tested included; week 1 against weeks 2-8, weeks 1 and 2 against weeks 3-8, and so forth. The best-fitting time model was that which separated week 1 (a1), from weeks 2-8 (a2). Thus we added age effect (a1, a2) in all datasets to test against other variables.

Interannual variation models. We used the global model Φ(Y*t) p(Y*t) to simulate parametric bootstrap for GOF, where Y is year variable. To test if survival varied annually we separated the data by year ($n_{2006} = 23$, $n_{2007} = 37$, and $n_{2008} = 27$).

Sex dependence models. We used the global model Φ(g*t) p(g*t) for GOF test, where g is sex to test whether survival probability differed between sexes. Out of 87 fledglings; 54 were of known sex (29 females and 25 males).

Helper(s) models. We tested survival of groups with helpers and those without from the brood independent data set (n =41), testing GOF with the global model Φ(h*t) p(h*t). Presence of helper(s) (n =19) is indicated by h and *noh* indicates the absence of helper(s) (n =22).

Individual covariate models. We used fledging date and body mass to predict the survival probability of individuals as continuous functions. We used logit-link function models and standardized the values of the covariates. Fledging date of each individual was calculated based on 1 January or Julian date (JD) (range = 63-208 days). We used one randomly chosen individual from each brood (n= 41) to avoid brood dependence effects.

We used body mass measurements (mass) of nestlings at ringing date (8-9 days old; 2-3 days before fledging) (range = 18.0-28.5 g). We also tested for sex differences in mass for known-sex birds using the Mann-Whitney U test. We excluded nestlings that were weighed at day 10, 11 or after leaving the nest from the analyses. Because nestlings in the same brood differed in body mass, we used data from all weighed nestlings (n = 45).

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. submitted.). 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.

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 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.

Model selection for timing and probability of dispersal

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 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 $\Delta QAIC_c$ of zero (Lebreton et al. 1992), while other models are expressed as some difference ($\Delta QAIC_c$) from zero. Models with $\Delta QAIC_c \leq 2$ 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 Φ(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 Φ(g*h*t) *p*(g*h*t) for testing bootstrap GOF where 'h' represents presence/absence of helper(s).

5. RESULTS

5.1) Post-fledging survival

Seventeen of 23 fledglings (74%) in 2006, 24 of 37 in 2007 fledglings (65%), and 22 of 27 (82 %) of fledglings in 2008 survived to independence; resulting in 72% actual survival rate. All fledglings from three years combined (*n* = 87) and the brood independent set (*n* = 41) fit the same best model for age effects Φ(a1,a2) *p*(a1,a2). This age effect model is 500 times more likely supported by the data than the global model Φ(t) *p*(t) based on the $QAIC_c$ weights (Table 1A). The largest effect on fledgling survival was related to fledgling age where Φ and *p* of age at first week (a1) had lower survival, while survival was higher and largely constant over the period from weeks 2-8 (a2). The probability of fledglings surviving (mean ± SE) the first week based on model averaging of the brood independent dataset was 0.78 ± 0.08, while the average survival estimates for weeks 2-8 was 0.98 ± 0.01. Cumulative survival probability (± SE) for the eight weeks post-fledging dependent period was 0.67 ± 0.01.

Interannual variation. Survival estimates including year effects indicate that fledglings experienced nearly identical rates of survival in different years. The year effect model only contributes 0.01 based on the $QAIC_c$ weights (model 9; Table 1B). The cumulative survival probability (± SE) during the dependent period from model averaging was 0.67 ± 0.02 during both 2006 (*n* = 23) and 2007 (*n* = 37), and 0.68 ± 0.02 in 2008 (*n* = 27).

Sex. There was no evidence of sex-biased survival (model 1-3; Table 2) and sex had little weight in the model (5%) (model 4; Table 2). Survival probability from model averaging during the first week for males (*n* =29) was 0.73 ± 0.08 and 0.72 ± 0.08 for females (*n* = 25).

Presence of helpers. Helpers (*n* =41) contributed 22 % to survival models when combined with age effects during the first week (model 7; Table 2). The best-fitting survival model included the age class effect (model 7; Table 2) which was 1.5 times and 3.2 times more supported than helper models (models 8 and 10; Table 2), and > 34 000 times more supported than the global model (model 12; Table 2) based on the $QAIC_c$ weights. The helper model combined with age effect suggested that fledglings in groups with helper(s) exhibit slightly higher survivorship than those in groups without helpers. The modest benefit of additional adults is apparent only during the first week post-fledging. During the first week post fledging, survival probabilities were 0.85 ± 0.10 and 0.79 ± 0.08 for fledglings with helpers and no helpers respectively. By the end of the dependent period, the cumulative survival probability for fledglings in groups with helper was 0.70 ± 0.01 and 0.68 ± 0.01 for those without helper(s).

Effects of individual covariates.

Body mass of nestlings at ringing date of male (mean ± SD = 23.11 ± 2.14; *n* =19) and female (mean ± SD = 23.36 ± 2.30, *n* =21) were not different (Mann-Whitney *U*-test, $z = -0.34$, $P = 0.73$). Based on three years combined data (*n* = 45); body mass has a positive effect on the probability of survival during the first week (model 3; Table 3). The interaction between body mass and age effect (model 3; Table 3) fit the data 14 times better than the global model (model 4; Table 3). During the first week after fledging, heavier individuals experience higher survival (Figure 1).

Fledging date of brood independent individuals from three years combined (*n* =41) affected neither the probability of survival nor resighting. The best fit survival model was largely the age class effect Φ (a1, a2), while fledging date had minimal support (model 10; Table 3). Fledging date was important only during the first week when early fledglings experienced higher survivorship than birds fledging later in t

5.2) Juvenile dispersal

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 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 4). 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 4).

Dispersal distances

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 4, 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).

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).

Probability of staying

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 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 5). The breeding interval model (model 1; Table 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 2a). 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 2a). 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 2a) which contributed 100% to the $QAIC_c$ weights. The best-fitting model (model 6; Table 5) was > 30,000 times more likely supported than the null and global models (models 9 and 10; Table 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 6). The most parsimonious model incorporated group size (model 6; Table 6) and was 19 times less likely supported than the best-fitting model of breeding season and sex effects (model 1; Table 6), while the best-fitting model was >35,000 times more likely supported than the global model (model 7; Table 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 2b). 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). 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) was 5.4% more likely supported by the data than the best-fitting helper model (model 9; Table 6). 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

6.1) Post-fledging survival

Puff-throated Bulbuls experience high survival during the 8-week post-fledging period (67%). The cumulative survival probability by the end of the dependent post-fledging period was similar to Seychelles Warblers (0.61; Brouwer 2006), White-throated Robins (0.67; Cohen and Lindell 2004), and Brown Thornbills (0.64; Green and Cockburn 2001), all of which are tropical or southern hemisphere species. This higher survivorship is notable in comparison to post-fledging survivorship rates detected in temperate birds; 0.43 in Wood Thrushes (Anders et al. 1997), 0.36 in Lark Buntings (Yackel Adams et al. 2006), and 0.13 in Great tits (Greño et al. 2008), though these studies relied on different criteria and different time scales (e.g. daily, weekly, or whole dependent period) and that not all studies in the temperate zone indicate lower post-fledging survival (Vega Rivera 1998).

The increased juvenile survivorship of tropical and southern hemisphere birds is often explained by the life history traits of smaller clutch sizes and prolonged parental care (Martin 1996, Russell et al. 2004). There is a growing body of evidence to suggest that tropical and southern hemisphere birds have 'slow' life histories relative to those in the northern hemisphere, i.e., smaller clutch sizes, extended parental care, and higher adult survival rates (Russell et al. 2004); the Puff-throated Bulbul clearly fits this paradigm. In addition, Martin (2002) suggested that adult survival is the primary driver in explaining increased parental care in southern and tropical groups. Accordingly, we find high adult survival rates in Puff-throated Bulbuls in our system (Sankamethawee, unpubl. data).

Studies of cooperatively breeding birds report both positive (Magrath 2001, Conner et al. 2004, Woxvold and Magrath 2005, Valencia et al. 2006), and negative effects (Brouwer et al. 2006) of group living on reproductive success and survival. In Apostlebirds, fledgling production and annual recruitment appear to result from the presence of active helpers rather than being associated with group size per se (Woxvold and Magrath 2005). Our results suggest a similar pattern in which helpers are associated with an increase in survival during the crucial first week leaving the nest, with the effect contributing 22% to survival (model 8; Table 2). The benefits of helping may not be restricted to food provisioning (Woolfenden 1978). Other likely benefits include increased anti-predation by alarm calling, mobbing, and warning of approaching predators for fledglings to find better cover (McGowan and Woolfenden 1989).

The critical period for survivorship success appears to be during the first week after birds leave the nest, a finding supported by other studies in both temperate (Sullivan 1989, Davies and Restani 2006, Berkeley et al. 2007), and tropical systems where high mortality rates are attributed to limited flying abilities (e.g. Green and Cockburn 2001, Cohen and Lindell 2004) that may result in predation (Sullivan 1989, Keedwell 2003, Berkeley 2007). The high mortality we observe during the first week suggests a potential area where helpers may enhance fledgling survival through predator warning and food provisioning. While we seldom found direct evidence of predation in our study (two juvenile kills across all three years), we suspect that predation is a key source of fledgling mortality because young birds are less capable of sustained flight and are naïve with respect to predators. We also see little evidence of weather induced mortality. Given the frequency of nest checks and observer effort it is unlikely we would have missed such an event. Starvation can also result in juvenile mortality, but fruit scarcity does not appear to be an issue during the nestling and post-fledgling periods based on fruit phenology data (Sankamethawee unpubl. data). However, we are unable to quantify fledgling mortality due to lack of food resources.

The positive relationship we detected between Puff-throated Bulbul nestling mass and survival during the first week after fledging (Figure 1) is consistent with others (Garnet 1981, Tinbergen and Boerlijst 1990, Monrós et al. 2002) who have shown that heavier nestlings experience a higher survivorship probability during the post-fledging period. Body mass and body condition of the young reflect the quality and quantity of parental care during both the nestling and fledgling stages. This may be particularly true for cooperative breeding birds as additional extended adult care improves juvenile body mass and condition. We observed helper Puff-throated Bulbuls feeding fledglings more frequently than nestlings (Wonkson unpubl. data), and additional food may result in improved fledgling health, though the contribution may be difficult to detect.

Sex was not associated with post-fledging survival in this study, however knowledge of sex-biased survival of juvenile forest birds is very limited, and our data adds to a rarely reported aspect of the post-fledging period. The absence of sex-associated effects contrasts with findings of one of the few studies on this topic where male Brown Thornbill fledglings, which are generally heavier, were more likely to survive to independence than lighter female fledglings (Green and Cockburn 2001). We found no significant difference between body mass of male and female nestlings; further indicating that sex is unlikely to be associated with fledgling survival and body mass is unlikely to be sex-dependent during the nestling stage in this species. However, nearly all studies which have found sex-biases in survival were conducted on nestlings (Røskaft and Slagsvold 1985, Arroyo 2002) or adult birds (Grüebler et al. 2008).

Although we focused on several questions related to juvenile survival, both female and territory quality may be important (Ligon and Ligon 1990) but were not addressed in this study. In our study system, some females raise young successfully to independence each year, regardless of her mate or assistance from helpers. For example, one female successfully raised two broods to independence in two consecutive years, which anecdotally suggests that individual quality and experience may influence juvenile survival. On the other hand, territory quality is also often discussed as a potential factor influencing reproductive success (Ligon and Ligon 1990) but has rarely been demonstrated (Legge 2000). Discerning breeder and/or territory quality is difficult due to confounding factors (Cockburn 1998, Legge 2000, Woxvold and Magrath 2005).

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 unpubl. data), 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.

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.

6.2) Juvenile dispersal

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.

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.

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.

7. LITERATURE CITED

Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson III. 1997. Juvenile survival in a population of Neotropical migrant birds. Conservation Biology 11:698-707.

Arroyo, B. 2002. Sex-biased nestling mortality in the Montagu's Harrier *Circus pygargus*. Journal of Avian Biology 33:455-460.

Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger. 2007. Post-fledging survival and movement in Dickcissels (*Spiza americana*): implications for habitat management and conservation. Auk 124:396-409.

Brockelman, W. Y. 1998. Long term ecological research plot for the study of animal diets in Khao Yai National Park, p. 307-310. *In* P. Poonswad [ed.], The Asian Hornbills: ecology and conservation. Thai Studies in Biodiversity No. 2.

Brouwer, L., D. S. Richardson, C. Eikenaar, and J. Komdeur. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. Journal of Animal Ecology 75:1321-1329.

Brown, J. L. 1987. Helping and Communal Breeding in Birds. - Princeton University Press, Princeton. Carmen, W. J. 2004. Noncooperative breeding in the California Scrub-Jay. Study in Avian Biology No. 28: Cooper Ornithology Society.

Cockburn, A. 1998. Evolution of helping behavior in cooperatively breeding birds. Annual Review of Ecology and Systematics 29:141-177.

Cockburn, A. 2004. Mating systems and sexual conflict. - In: Koenig, W. D., Dickinson, J. L. (eds.), Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, pp. 81-101.

Cockburn, A., H. L.Osmond, R. A. Mulder, D. J. Green and M. C. Double. 2003. Divorce, dispersal and incest avoidance in the cooperatively breeding superb fairy-wren *Malurus cyaneus*. Journal of Animal Ecology 72: 189-202.

Cockburn, A., H. L. Osmond, R. A. Mulder, M. C. Double and D. J. Green. 2008. Demography of male reproductive queues in cooperatively breeding superb fairy-wrens *Malurus cyaneus*. Journal of Animal Ecology 77: 297-304.

Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling White-throated Robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. Auk 121:404-414.

Conner, R. N., D. Saenz, R. R. Schaefer, J. R. McCormick, D. C. Rudolph, and D.B. Burt. 2004. Group size and nest success in Red-cockaded Woodpeckers in the West Gulf Coastal Plain: helpers make a difference. Journal of Field Ornithology 75:74-78.

Cooch, E., and G. White. [on line]. 2008. Program MARK: A gentle introduction. (7th edition), <http://www.phidot.org/software/mark/docs/book/> (23 December 2008).

Covas, R. and M. Griesser. 2007. Life history and the evolution of family living in birds. Proceeding of the Royal Society London B 274: 1349-1357.

Curry, R. L. and P. R. Grant. 1990. Galapagos Mockingbirds: territorial cooperative breeding in a climatically variable environment. In: P. B. Stacey and W. D. Koenig [eds.], Cooperative breeding in birds: long-term studies of ecology and behaviour. Cambridge University Press, Cambridge, pp. 291-331.

Davies, J. M., and M. Restani. 2006. Survival and movements of juvenile Burrowing Owls during the post-fledging period. Condor 108:282-291.

Daniels, S. J. and J. R. Walters. 2000. Inbreeding depression and its effects on natal dispersal in Red-cockaded Woodpeckers. Condor 102: 482-491.

Doerr, E. D., and V. A. J. Doerr. 2006. Comparative demography of treecreepers: evaluating hypotheses for the evolution and maintenance of cooperative breeding. Animal Behaviour 72:147-159.

Garnett, M. C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. Ibis123: 31-41.

Eikenaar, C., D. S. Richardson, L. Brouwer and J. Komdeur. 2008. Sex biased natal dispersal in a closed, saturated population of Seychelles warblers *Acrocephalus sechellensis*. Journal of Avian Biology 39: 73-80.

Ekman, J. and M. Griesser. 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. - Proc. R. Soc. B 269: 1709-1713.

Ekman, J., A. Bylin and H. Tegelström. 1999. Increased lifetime reproductive success for Siberian jay (*Perisoreus infaustus*) males with delayed dispersal. Proceeding of the Royal Society London B 266: 911-915.

Ekman, J., A. Bylin and H. Tegelström. 2000. Parental nepotism enhances survival of retained offspring in the Siberian jay. - Behav. Ecol. 11: 416-420.

Ekman, J., J. L. Dickinson, B. J. Hatchwell and M. Griesser. 2004. Delayed dispersal. In: W. D. Koenig and J. L. Dickinson [eds], Ecology and Evolution of Cooperative Breeding in Birds. Cambridge University Press, Cambridge, pp. 48-66.

Green, D. J., and A. Cockburn. 2001. Post-fledging care, philopatry and recruitment in Brown Thornbills. Journal of Animal Ecology 70:505-514.

Greenwood, P.J. 1980. Mating system, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 1140-1162.

Griesser, M. 2003. Nepotistic vigilance behaviour in Siberian Jay parents. Behavioral Ecology 14:246-250.

Griesser, M. and J. Ekman. 2004. Nepotistic alarm calling in the Siberian jay (*Perisoreus infaustus*). Animal Behaviour 67: 933-939.

Grüebler, M. U., H. Schuler, M. Müller, R. Spaar, P. Horch, and B. Naef-Daenzer. 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a Meadow bird. Biological Conservation 141:3040–3049.

Keedwell, R. J. 2003. Does fledging equal success? Post-fledging mortality in the Black-fronted Tern. Journal of Field Ornithology 74:217-221.

Kokko, H. and J. Ekman. 2002. Delayed dispersal as a route to breeding: territorial inheritance, safe havens, and ecological constraints. American Naturalists 160: 468-484.

Kokko, H. and R. A. Johnstone. 1999. Social queuing in animal societies: a dynamic model of reproductive skew. Proceeding of the Royal Society London B 266: 571-578.

Krementz, D. G., J.D. Nichols, and J. E. Hines. 1989. Post-fledging survival of European Starlings. Ecology 70:646-655.

Lebreton, J-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67-118.

Legge, S. 2000. The effects of helpers on reproductive success in the Laughing Kookaburra. Journal of Animal Ecology 69:714-724.

Ligon, J. D., and S. H. Ligon. 1990. Green Woodhoopoes: life history traits and sociality, p. 33-65. In P. B. Stacey and W. D. Koenig [eds.], Cooperative breeding in birds: long-term studies of ecology and behaviour. Cambridge University Press, Cambridge.

Magrath, R. D. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. Journal of animal Ecology 60:335-351.

Magrath, R. D. 2001. Group breeding dramatically increases reproductive success of yearling but not older female Scrubwrens: a model for cooperatively breeding birds? Journal of Animal Ecology 70:370-385.

Martin, T. E. 1996. Life history evolution in tropical and south temperate birds: what do we really know? Journal of Avian Biology 27:263-272.

Martin, T. E. 2002. A new view of avian life-history evolution tested on an incubation paradox. Proceedings of the Royal Society of London Series B 269:309-316.

McGowan, K. J., and G. E. Woolfenden. 1989. A sentinel system in the Florida Scrub-Jay. Animal Behaviour 37: 1000-1006.

Miller, K. E. and J. A. Smallwood. 1997. Natal dispersal and philopatry of Southeastern American Kestrels in Florida. Wilson Bull. 109: 226-232.

Monrós, J. S., E. J. Belda, and E. Barba. 2002. Post-fledging survival of individual Great Tits: the effect of hatching date and fledging mass. Oikos 99:481-488.

Naef- Daenzer, B., F. Wiumer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. Journal of Animal Ecology 70:730-738.

Pasinelli, G. and J. R. Walters. 2002. Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. Ecology 83: 2229-2239.

Pierce, A. J., and K. Pobprasert. 2007. A portable system for continuous monitoring of bird nests using digital video recorders. Journal of Field Ornithology 78:322-328.

Pierce, A. J., K. Tokue, K. Pobprasert, and W. Sankamethawee. 2007. Cooperative breeding in the Puff-throated Bulbul *Alophoixus pallidus* in Thailand. Raffles Bulletin of Zoology 55:199-201.

Røskaft, E., and T. Slagsvold. 1985. Differential mortality of male and female offspring in experimentally manipulated broods of the Rook. Journal of Animal Ecology 54:261-266.

Rowley, I. and E. Russell. 1997. Fairy-Wrens and Grasswrens: Maluridae. Oxford University

Press, Oxford.

Russell, E. M., Y. Yom-Tov, and E. Geffen. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behavioural Ecology 15:831-838.

Sankamethawee, W., G. A. Gale and B. D. Hardesty. Submitted. Post-fledging survival of the cooperatively breeding Puff-throated Bulbul (*Alophoixus pallidus*). Condor.

Stutchbury, B. J. M., and E. S. Morton. 2001. Behavioral Ecology of Tropical Birds. London, Academic Press.

Tinbergen, J. M., and M. C. Boerlijst. 1990. Nestling weight and survival in individual Great Tits (*Parus major*). Journal of Animal Ecology 59:1113-1127.

Valencia, J., C. De La Cruz, J. Carranza, and C. Mateos. 2006. Parents increase their parental effort when aided by helpers in a cooperatively breeding bird. Animal Behaviour 71:1021-1028.

Vega Rivera, J. H., J. H. Rappole, W. J. McShea, and C. A. Haas. 1998. Wood Thrush post-fledging movements and habitat use in Northern Virginia. Condor 100:69-78.

Verboven, N., and M. E. Visser. 1998. Seasonal variation in local recruitment of Great Tits: the importance of being early. Oikos 81:511-524.

Wheelwright, T. N., K. A. Tice, and C. R. Freeman-Gallant. 2003. Post-fledging parental care in Savannah Sparrows: Sex, size, and survival. Animal Behaviour 85:435-443.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. - Bird Study 46 (Supplement): 120-139.

Woolfenden, G. E. 1978. Growth and survival of young Florida Scrub-Jays. Wilson Bulletin 90:1-18.

Woolfenden, G., and J. Fitzpatrick. 1984. The Florida Scrub-Jay: demography of a Cooperative Breeding Bird. Princeton, New Jersey: Princeton University Press.

Woxvold, I. A., and M. J. L. Magrath. 2005. Helping enhances multiple components of reproductive success in the cooperatively breeding Apostlebird. Journal of Animal Ecology 74:1039-1050.

Woxvold, I. A., Adcock, G. J. and Mulder, R. A. 2006. Fine-scale genetic structure and dispersal in cooperatively breeding Apostlebirds. Molecular Ecology 15: 3139-3146.

Yáber, M. C. and Rabenold, K. N. 2002. Effects of sociality on short-distance, female-biased dispersal in tropical wrens. Journal of Animal Ecology 71: 1042-1055.

Yackel Adam, A. A., S.K. Skagen, and J. A. Savidge. 2006. Modeling post-fledging survival of Lark Buntings in response to ecological and biological factors. Ecology 87:178-188.

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 Biodiversity Research and Training Program (BRT_T350006), and the Royal Golden Jubilee Ph.D. Program (PHD/0240/2547).

8. PROJECT OUTPUTS

Papers submitted to international journals:

1) Sankamethawee, W., G.A. Gale, and B. D. Hardesty. Post-fledgling survival of the cooperatively breeding Puff-throated Bulbul (*Alophoixus pallidus*)

Status *—accepted pending minor revision in* CONDOR

2) Sankamethawee, W., B. D. Hardesty, and G.A. Gale. Natal philopatry and sex-biased dispersal in the cooperatively breeding Puff-throated Bulbul

Status—submitted and under reviewing in JOURNAL OF AVIAN BIOLOGY

Papers in preparation

1) Sankamethawee, W., A. J. Pierce, G. A. Gale, and B. D. Hardesty. Annual survival of a cooperatively breeding bird in an evergreen forest, Thailand. Target journal: BIOTROPICA

2) Sankamethawee, W., S. Tanasarnpaiboon, J. Khoonwongsa, and G.A. Gale. Nest site characteristics and nesting success of a cooperatively breeding tropical forest passerine, Thailand. Target journal: BIOTROPICA

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

9. APPENDICES

Table 1. Summary of model selection statistics of age effects (A) on survival and resighting probabilities, and interannual effects (B) during the post-fledging period of Puff-throated Bulbul at Khao Yai National Park, Thailand (2006-2008) based on a brood independent dataset (n=41). Models are ranked by quasi Akaike's information criterion corrected for small sample sizes ($QAIC_c$). Chosen model candidates based on the relative $QAIC_c$ weights of the model of interest to the best-fitting model, the null model, and the global models. Models are presented with the number of parameters (K), differences in $QAIC_c$ scores relative to the top-ranked model ($\Delta QAIC_c$), and $QAIC_c$ weights. Variables are coded as: age at first week post-fledging (a1), age during week 2 to week 8 post-fledging (a2), constant (.), year (Y), and time dependence (t).

No.	Model structure	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ Weights	K
A	*Age effects*				
1	Φ(a1,a2) p(a1,a2)	203.48	0.00	0.54	4
2	Φ(a1,a2) p(.)	204.14	0.66	0.39	3
3	Φ(a1,a2) p(t)	208.24	4.76	0.05	10
4	Φ(.) p(.)	212.42	8.94	0.01	2
5	Φ(t) p(t)	216.13	12.65	0.00	15
B	*Interannual effects*				
6	Φ(a1,a2) p(t)	487.56	0.00	0.67	10
7	Φ(a1,a2) p(a1,a2)	489.62	2.06	0.24	4
8	Φ(a1,a2) p(Y*t)	492.20	4.64	0.07	26
9	Φ(Y*(a1,a2) p(Y)	495.22	7.66	0.01	9
10	Φ(.) p(.)	511.78	24.22	0.00	2
11	Φ(Y*t) p(Y*t)	528.56	41.00	0.00	46

Table 2. Summary of model selection statistics of gender effects (*n* =45) (A), and presence of helpers (brood independent dataset, n = 41) (B) on survival and resighting probabilities during the post-fledging period of the Puff-throated Bulbul at Khao Yai National Park, Thailand. Models are chosen, ranked and coded as in Table 1. Additional variables are coded as gender (g), presence of helper(s) (h), and no helper (noh).

No.	Model structure	QAIC_c	$\Delta\mathrm{QAIC}_c$	QAIC_c Weights	*K*
A	*Gender*				
1	Φ(a1,a2) *p*(a1,a2)	238.03	0.00	0.45	4
2	Φ(a1,a2) *p*((a1,a2)*g)	240.30	2.27	0.15	6
3	Φ(a1,a2) *p*(a1(.), (a2*g)	242.02	3.99	0.06	6
4	Φ(a1*g), a2(.) *p*(.)	242.26	4.23	0.05	4
5	Φ(.) *p*(.)	251.28	13.25	0.00	2
6	Φ(g*t) *p*(g*t)	278.45	40.42	0.00	30
B	*Presence of helper(s)*				
7	Φ(a1,a2) *p*(h(.), noh*(a1,a2))	198.75	0.00	0.34	5
8	Φ((h*a1), a2(.) *p*(h(.), noh*(a1,a2))	199.61	0.86	0.22	5
9	Φ(a1,a2) *p*(h*(a1,a2))	200.86	2.11	0.12	6
10	Φ(h*a1), a2(.) *p*(h*(a1,a2))	201.10	2.35	0.11	6
11	Φ(.) *p*(.)	210.29	11.54	0.00	2
12	Φ(h*t) *p*(h*t)	243.41	44.66	0.00	31

Table 3. Summary of model selection statistics with individual covariates; nestling mass (A) and fledging date (B) on survival and resighting probabilities for post-fledging Puff-throated Bulbul at Khao Yai National Park, Thailand. Models are chosen, ranked and coded as in Table 1. Additional variables are coded as body mass of nestling at 8-9 days (mass), Fledging date (JD).

No.	Model structure	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ Weights	*K*
B	*Nestling mass*				
1	Φ(a1,a2) p(t)	290.69	0.00	0.36	9
2	Φ(t) p(t)	290.75	0.06	0.35	12
3	Φ(mass*a1), a2(.) p(t)	291.34	0.65	0.26	10
4	Φ(mass*t) p(mass*t)	296.66	5.97	0.02	22
5	Φ(a1,a2) p(a1,a2)	301.56	10.87	0.00	4
6	Φ(.) p(.)	327.39	36.70	0.00	2
A	*Fledging date*				
7	Φ(a1,a2) p(t)	315.80	0.00	0.66	10
8	Φ(a1,a2) p(a1,a2)	318.11	2.31	0.21	4
9	Φ(t) p(t)	321.19	5.39	0.04	15
10	Φ(a1*JD), a2(.) p(.)	323.14	7.34	0.02	4
11	Φ(JD*t) p(JD*t)	330.38	14.58	0.00	22
12	Φ(.) p(.)	337.29	21.49	0.00	2

Table 4. 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	12	4	4
[a]Dispersal distance range (excluding philopatric birds)	2-7	1-2	1
[a]Mean territories crossed (excluding philopatric birds) ± SD	3.9 ± 1.9	1.2 ± 0.6	-
[a]Mean territories crossed (including philopatric birds) ± SD	3.3 ± 2.3	0.5 ± 0.7	-
[b]Mean territories crossed (including birds never located)	3.4 ± 1.3	1.0 ± 1.5	2.7 ± 1.4

Table 5. 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	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ 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

Table 6. 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	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ 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

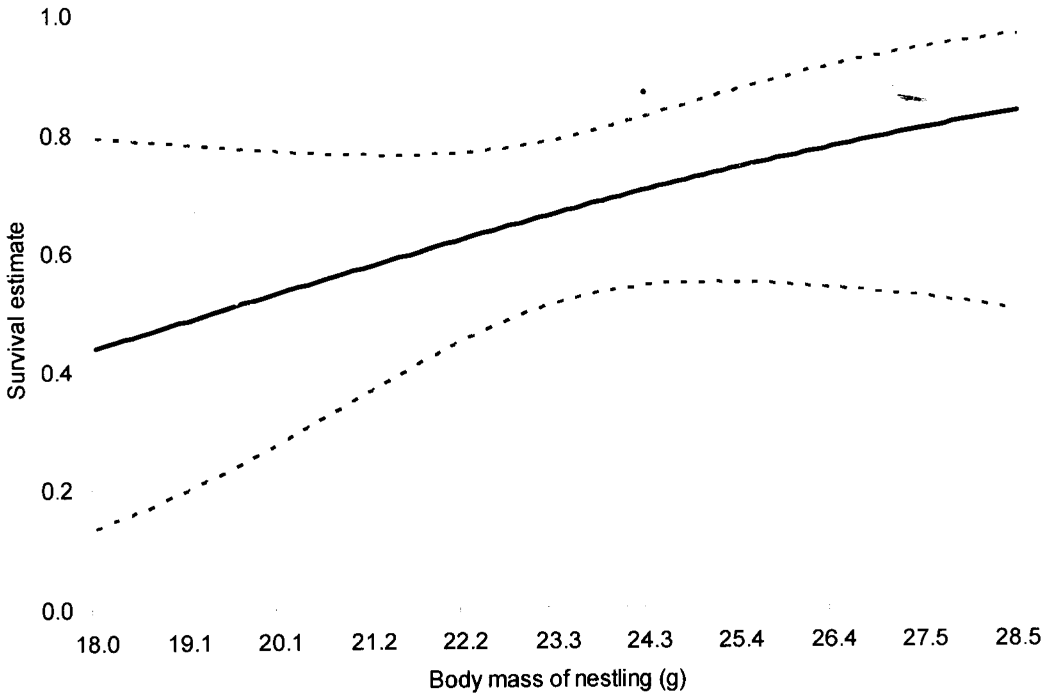

Figure 1. Predicted survival probabilities (± 95% CI) during the first week post-fledging of Puff-throated Bulbuls with different nestling body masses. Nestlings were weighed 2-3 days prior to fledging.

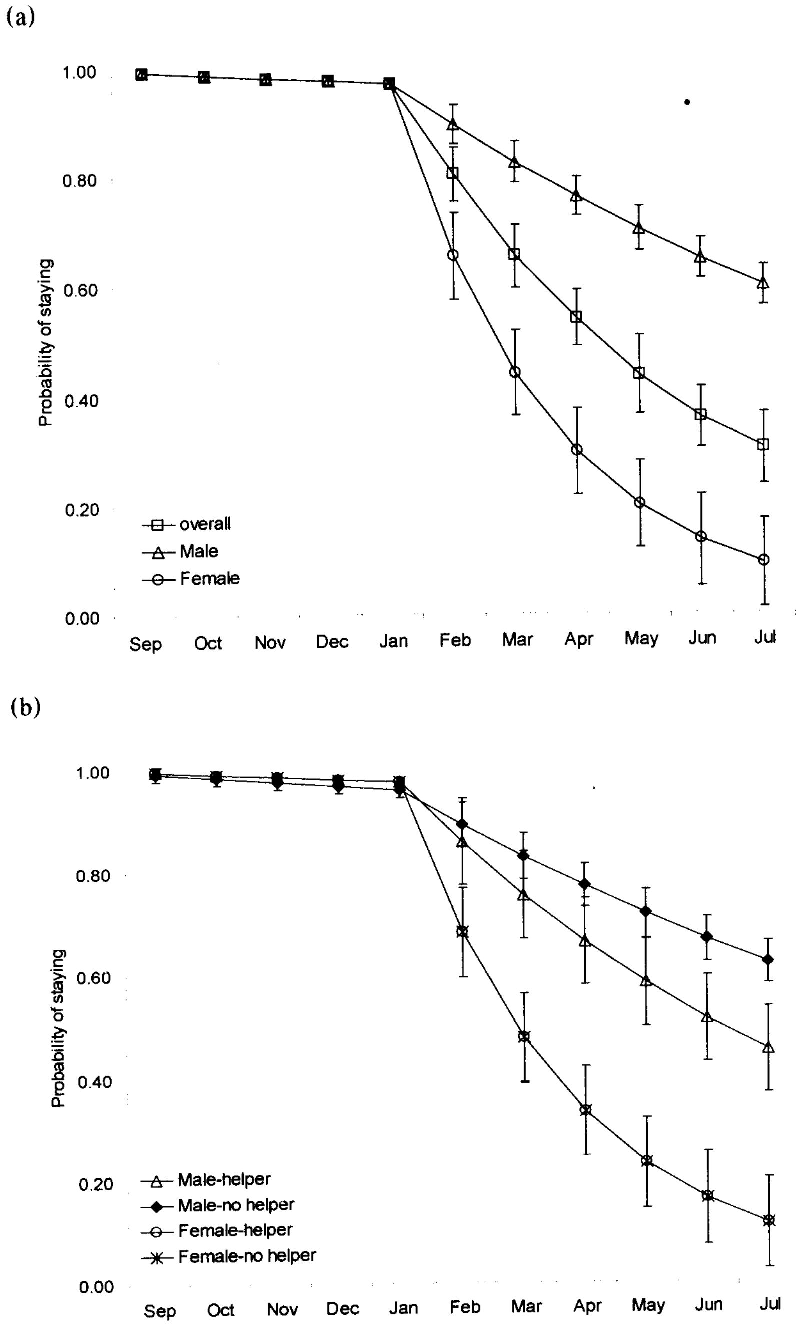

Figure 2. Probability of staying (cumulative survival probability (± SE) in natal territory of offspring Puff-throated Bulbuls. Part (a) Demonstrates the overall and sex-dependent patterns, (b) demonstrates the effects of the presence/absence of helpers. Five monthly intervals from August to January 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.

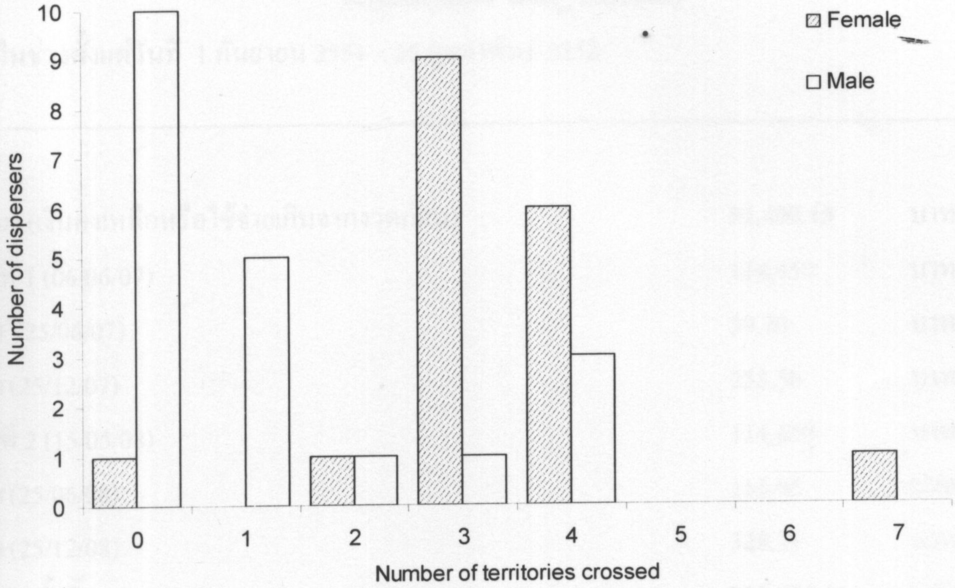

Figure 3. Frequency of natal dispersal distances of known sex offspring Puff-throated Bulbuls (18 females and 20 males) including known dispersal locations (n = 11), natal philopatric (n =11), and individuals never relocated, estimated from the minimum possible dispersal distance (n =16). The number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

สรุปรายงานการเงิน (Final budget report)

โครงการวิทยานิพนธ์ เรื่อง Post-fledging survival and juvenile dispersal of the cooperative breeding Puff-throated Bulbul (*Alophoixus pallidus*)

(รหัสโครงการ BRT_T350006)

รายงานในช่วงตั้งแต่วันที่ 1 กันยายน 2551 – 28 กุมภาพันธ์ 2552

รายรับ

ยอดยกมา (เงินคงเหลือหรือใช้จ่ายเกินจากงวดก่อน)	**52,400.15**	บาท	
เงินงวดที่ 1 (06/06/07)	114,450	บาท	
ดอกเบี้ย (25/06/07)	39.70	บาท	
ดอกเบี้ย (25/12/07)	253.50	บาท	
เงินงวดที่ 2 (15/05/08)	114,650	บาท	
ดอกเบี้ย (25/06/08)	156.95	บาท	
ดอกเบี้ย (25/12/08)	328.21	บาท	
รวมรายรับทั้งสิ้น	229,878.36	บาท	(1)

รายจ่าย

1. หมวดค่าตอบแทน 52,060 (ค่าธรรมเนียมการโอน 60) บาท

รวมรายจ่ายงวดที่ 1	54,565	บาท
รวมรายจ่ายงวดที่ 2	49,020	บาท
รวมรายจ่ายงวดที่ 3	73,565	บาท
รวมรายจ่ายงวดที่ 4	52,060	บาท

รวมรายจ่ายทั้งสิ้น	**229,210.00**	**บาท (2)**
ยอดคงเหลือ	**668.36**	**บาท (1) – (2)**

ลงนาม ....

(Dr. George A. Gale)

อาจารย์ที่ปรึกษา

วันที่ 6/ พ.ค. / 2552

ลงนาม ....

(นางสาววังวร สังฆเมธาวี)

นักศึกษา

วันที่ 6/ พ.ค. / 2552