Influence of food availability and distribution on the movement patterns of a forest avian frugivore, the puff-throated bulbul (*Alophoixus pallidus*)

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Abstract: Bulbul species (family Pycnonotidae) are important seed dispersers in Asian forests, but almost nothing is known of their movement patterns inside intact forest, which are likely to impact forest dynamics. We examined the movement patterns of the forest-dwelling puff-throated bulbul (*Alophoixus pallidus*) in relation to fruit productivity and distribution of fruiting trees/lianas in an evergreen forest in north-eastern Thailand. Movement patterns of 10 groups were precisely mapped by following colour-ringed individuals in each group 4 h mo^{-1} for 1 y. We evaluated fruit productivity and dispersion of fruiting trees/lianas based on monthly phenologies. There were clear seasonal fluctuations in fruit availability, which appeared to affect movement patterns, particularly distance moved between fruiting trees, time spent feeding and food selection. When fruit availability was low, bulbuls spent more time on average at a given food plant and moved longer distances between fruiting plants than compared with periods of higher fruit availability (low availability: 58 s, 83.2 m; high availability: 10 s, 43.4 m). This study points to the importance of seasonal availability of fruit resources on frugivore movement patterns. Seasonal dynamics of movement may be useful for understanding interactions between fruiting trees and their dispersers, and forest tree recruitment patterns.

Key Words: bulbuls, foraging patterns, fruit availability, resource distribution, Thailand, tropical birds

INTRODUCTION

The behaviour of fruit-eating animals has important consequences for the evolution of plants with zoochorous modes of seed dispersal (Wheelwright 1991). Factors such as diet or stage of breeding cycle, which have been reported as having significant effects on animal movements, will influence where the seeds land and therefore the reproductive success of the plants being dispersed (Fogden 1972, Hoppes 1987, Karubian & Duraes 2009, Levey 1987, Wheelwright 1991). Movement patterns can also provide valuable information about the distribution of resources available to an animal or similarly, movement patterns may be predictable from the spatial distribution of resources (Murray 1988, Westcott & Graham 2000).

In the wet tropics, approximately 70% of plant species have zoochorous modes of seed dispersal (Au *et al.* 2006, Corlett 1998, Herrera 2002) and birds typically comprise a large majority of these animal dispersers (Corlett 1998, Kitamura *et al.* 2004). In tropical East Asian forests, it is estimated that 85% of fleshy-fruited plant species are eaten and seeds dispersed by birds (Corlett 2009); similarly in neotropical forests birds are dispersers for approximately 75% of tree species (Wenny & Levy 1998). However, we typically know relatively little about the individual movement patterns of tropical frugivorous birds in relation to available fruit resources.

In tropical East Asia, based on current phylogenies, bulbuls (family Pycnonotidae) are represented by 55 species, accounting for 2% of the region's avifauna and are thought to be particularly important seed dispersers (Corlett 2009). However, while bulbuls are abundant and have a significant impact on patterns of seed dispersal in the entire region, there are almost no data focusing on the

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movement patterns of this group as key dispersers within forested habitats.

The objective of this study was to investigate the movement patterns of a forest-interior bulbul during the course of a year in relation to variation in fruit resources. We describe movement patterns in relation to fruit availability and dispersion within home ranges of the puff-throated bulbul (*Alophoixus pallidus* Swinhoe). We chose this species because it is widely distributed in the Asian region (Robson 2000) and abundant, at least, locally in the study site, Khao Yai National Park, Thailand (Gale *et al.* 2009). We predicted that: (1) total feeding range would decrease with increasing availability and aggregation of fruit resources, (2) average distances moved between fruit foraging locations would decrease with increasing availability and increasing aggregation of fruit resources, and (3) time spent foraging on individual trees would decrease with increasing availability and increasing aggregation of fruit resources.

METHODS

Study site

The study was conducted on the 30-ha Mo-singto Long-Term Biodiversity Research Plot (101°22'E, 14°26'N), Khao Yai National Park (KYNP; 2168 km^2), Thailand. The average temperature ranges from 17 °C in December and January to 28 °C in April and May. The average annual rainfall is 2554 mm, most of which falls between May and October; the dry season occurs from November to February (*c.* 7% of days with rain) (Khao Yai Project, unpubl. data).

The plot comprises a series of ridges and valleys with an altitudinal range of 730–860 m asl. The vegetation is mostly old-growth evergreen forest, dominated by fleshy-fruited trees with a small area of secondary forest at the north edge of the plot (Brockelman 1998). The plot is laid out on a 20 × 20-m grid. All trees with diameter at breast height (dbh) ≥ 1 cm have been identified, labelled with unique identification numbers, and mapped in a GIS with a precision of at least ± 1 m (Brockelman 1998).

Study species

The range of the puff-throated bulbul (*Alophoixus pallidus* Swinhoe) includes Cambodia, China, Laos, Myanmar, Thailand and Vietnam. It is a common resident of evergreen forest of northern and north-eastern Thailand (Lekagul & Round 1991) and is the most abundant bird species on the study plot (Gale *et al.* 2009). In KYNP, it has also been identified as the most common avian consumer of fruit (Kitamura *et al.* 2002). It lives in pairs or in groups of three to seven birds, defending a territory and foraging together (Pierce *et al.* 2004, Sankamethawee *et al.* 2009). Based on a study of faecal samples as well as direct observations of fruiting trees (Sankamethawee *et al.* in press), it consumes a wide variety of fruits (> 100 species). *Alophoixus pallidus* forages in the lower to middle canopy with an average foraging height of 9.4 m (range = 1–15 m) within an average home range of approximately 2.2 ha (Tanasarnpaiboon, unpubl. data). It ranges primarily in the forest interior, foraging rarely in non-forest habitat (Chaikuad, unpubl. data). It occasionally joins mixed-species bird flocks feeding on insects (McClure 1974, Nimnuan *et al.* 2004). Approximately 30 groups occupy the study area, such that all groups are surrounded by neighbours. Of these, 10 groups occupying the core of the Mo-singto plot were chosen for this intensive study.

Colour-ringing was initiated in January 2003 as part of a long-term study on the Mo-singto plot such that at the time of this work nearly all the members of the 10 focal groups could be individually identified. Unique combinations of two to three colour rings and one numbered aluminium ring from the Royal Thai Forest Department (currently the Department of National Parks, Wildlife and Plant Conservation) allowed for individual identification. Faecal samples were collected during the course of ringing to at least partly determine food types consumed by *A. pallidus* during the study period.

Plant phenology

We collected phenology data once per month on both trees and lianas, which we knew were part of the puff-throated bulbul diet based upon faecal samples and direct observations conducted on the plot (Sankamethawee *et al.*, in press). The exact location and dbh of each individual tree was obtained from the Mo-singto tree database referred to above. Monthly surveys were conducted in each territory of the 10 focal groups on three parallel 100 × 20-m belt-transects separated from one another by 20 m. Within the transects we monitored a total of 280 randomly selected individuals from 20 species (14 trees per species) of potential food trees with dbh ≥ 10 cm (range = 10–116 cm). For lianas we selected 226 stems from 14 species (~16 stems per species) with a dbh ≥ 1 cm (range = 1–44 cm). We counted and measured the basal area of all liana stems present in each transect. Percentage of fruit presence in the crown was recorded based upon a five-point score where 0 = no fruit, 1 = 1–25%, 2 = 26–50%, 3 = 51–75% and 4 = > 76% (Ragusa-Netto 2002).

Fruit productivity

Monthly fruit productivity for both fruiting trees and lianas were estimated following Savini *et al.* (2008):

$$\text{Fruit productivity} = \sum_{k=1}^{n} D_k B_k P_{km} W_k N_k$$

Where D_k is the density of species k in the area, B_k is the mean basal area of species k in the area, P_{km} is the percentage of observed trees of species (k) that produce ripe fruit in a given month (m), W_k is the mass of fruit for species k (Kitamura *et al.* 2002) and N_k the amount of fruit in the crown in 1 m^3 of species k. The number of fruits available in 1 m^3 of the crown was estimated visually and grouped into categories of abundance using the following group midpoints: 10, 20, 50, 100, 300, 500 or 1000 fruits. There were several limitations to measuring liana crown volume and counting fruit per twig/branch to estimate fruit productivity, thus liana fruit productivity in this study was estimated by the same method as fruiting trees even though the relationship between stem diameter and crown size (or fruit crop size) could not be clearly defined. Productivity of lianas followed the same methods as for fruiting trees where the basal area for lianas was estimated from the stem dbh. The diameter measurement point followed Gerwing *et al.* (2006) in which all stems that emerge more than 130 cm from the main root were measured.

Dispersion of fruiting trees and lianas

In order to estimate fruiting tree and liana dispersion, the belt transects were divided into 20 × 20-m sections. Dispersion of fruiting trees and lianas was calculated within the transect grid using the ratio of the variance to the mean of the monthly number of trees in fruit in the transect grids: the coefficient of dispersion (CD) following Chapman *et al.* (1992) and Chapman *et al.* (1995). When the CD > 1 fruiting trees are considered to be clumped; CD < 1 indicates fruiting trees are widely dispersed and when CD = 1 fruiting trees are randomly dispersed.

Movement patterns

Four of the ten focal groups of birds were randomly selected to be followed on a particular day. Their locations and feeding activities were recorded by following a focal animal from each group for a total of 4 h mo^{-1}. The 4 h were divided into 2-h observation periods conducted every 2 wk. The observations were conducted during May 2007 to April 2008, with the exception of September when no data were collected. The observations started when at least one individual in a group was found in their home range. The timing of the observations was started and finished within one of four time intervals: early morning (06h30–09h00), late morning (09h00–12h00), early afternoon (12h00–15h00) and late afternoon (15h00–18h00). Group composition was also recorded. When the birds were followed, tree numbers were used to precisely reference their locations and their true movement distances by georeferencing to the plot grid. The grid was corrected for topography.

When the bulbuls were feeding on a fruiting tree during the observation period, the first record was started when the first fruit was fed upon until they left the tree or stopped feeding. The numbers of fruit fed upon were also recorded based only on clearly visible events. The frequency of feeding events on insects was also recorded.

Data analysis

Bulbul home ranges were drawn based on the locations of colour-ringed birds, which were observed as part of the long-term study from 2003–2008. The areas were drawn using the 95% Minimum Convex Polygon (MCP) command in ArcView 3.2a (Boitani & Fuller 2000). Each home range was calculated from at least 470 observation points per group; group members nearly always forage together. The observed travel routes were mapped in a GIS (Animal Movement extension of ArcView). The association of fruit availability with movement patterns (feeding range, distance moved), and time spent feeding were examined using Spearman rank correlation coefficients for both independent groups as well as averaged data from all 10 bulbul groups combined. We also examined differences in distances moved and time spent on fruiting trees between seasons, breeding (February–August) and non-breeding (September–January) by using t-tests based on monthly averages from individual groups as well as all 10 groups combined. The area of the monthly range of movements was estimated based on 95% MCPs. The statistical analysis was conducted using R version 2.8.1.

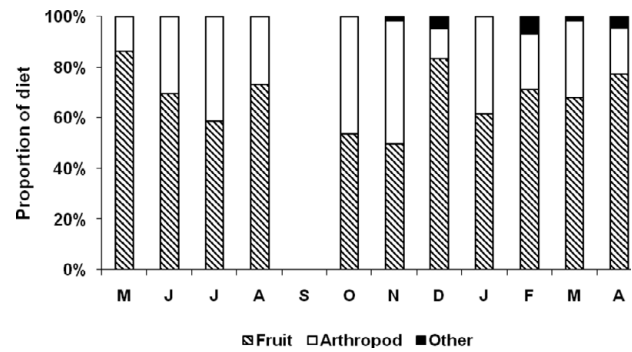### RESULTS

Fruit availability

During the 1-y study period, 280 fruiting trees from 20 species and 125 fruiting lianas from 14 species were monitored. There were clear seasonal fluctuations in fruit availability based on monthly averages of the 10 groups of *A. pallidus* combined. Overall, June had the highest fruit productivity (FP = 245) and the highest coefficient of dispersion (CD = 1.84) indicating greater clumping. Fruit productivity was lowest in January (FP = 29) and most widely dispersed in December (CD = 0.88). The
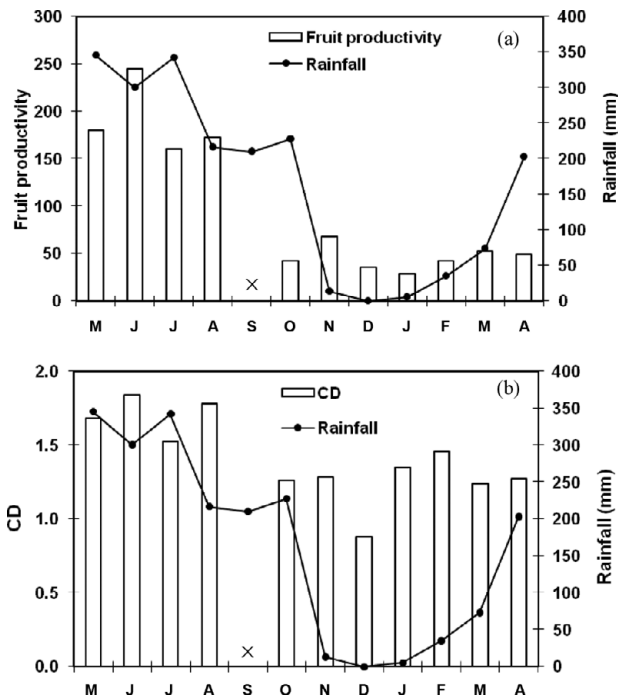
Figure 1. Relationship between total rainfall by month and fruit productivity (a) and the coefficient of dispersion (CD) (b). Fruits refer only to species fed upon by *Alophoixus pallidus*. Data collected from 10 *A. pallidus* groups on the Mo-singto Plot, KhaoYai National Park, Thailand during May 2007 to April 2008 ('x' indicates no data were collected during September 2007).

Figure 2. The proportion of different food types (fruit, arthropod, other (typically nectar or small lizards)) taken by *Alophoixus pallidus*. Number of feeding observations during this study from May 2007 to April 2008 were 58, 53, 92, 30, 0, 95, 132, 103, 128, 104, 122 and 136 respectively with no data collected during September 2007.

average fruit availability had two distinct periods during our study, with fruit being relatively more abundant from May to August 2007 during the wet season, followed by a notable decline and another period of little change between October 2007 and April 2008 through the dry season (Figure 1). On average, fruit of most species were available for 12 wk, however, one tree species *Gironniera nervosa* (Ulmaceae) and one liana species *Dissochaeta divaricata* (Melastomataceae) were available year round. Furthermore, *Gironniera nervosa* was fed upon by the bulbuls every month (Appendix 1). *Alophoixus pallidus* ate more fruit than other items. However during October and November after the end of the wet season, the proportion of non-fruit (primarily arthropods and nectar/flower parts) was nearly equal to that of fruit (Figure 2).

Overall, there was a significant positive correlation between monthly fruit productivity and the monthly coefficient of dispersion ($r_s = 0.74$, $P = 0.009$) using data for all 10 groups combined, such that when fruit abundance was low, fruiting trees/lianas were more spatially dispersed than during the periods of higher fruit productivity. Monthly rainfall was also significantly and positively correlated with monthly fruit productivity and coefficient of dispersion ($r_s = 0.72$, $P = 0.012$; $r_s = 0.68$, $P = 0.021$, respectively).

Feeding range in relation to resource

The average percentage of the home range covered during the monthly 4-h observation periods changed notably through the year. February was the month with the largest range while August was the month with the smallest range (Table 1). For only one group was there a significant correlation between monthly range of movement and the coefficient of dispersion ($r_s = -0.74$, $P = 0.009$), but six of the remaining nine had trends in the same direction although the overall correlation was not significant ($r_s = -0.47$, $P = 0.14$). There was no significant correlation between fruit productivity and the monthly range of movement for any of the different bulbul groups alone or combined ($r_s = -0.33$, $P = 0.32$) nor were there any consistent trends (r_s was < 0 for 4 of the 10 groups). There was no correlation between the median distance moved between fruiting trees and median feeding range per unit time ($r_s = 0.60$, $P = 0.18$) nor any correlation between median time spent on a fruiting tree and ranging area ($r_s = 0.47$, $P = 0.14$). There was also no correlation between median total distance moved and median feeding range per unit time ($r_s = 0.47$, $P = 0.15$).

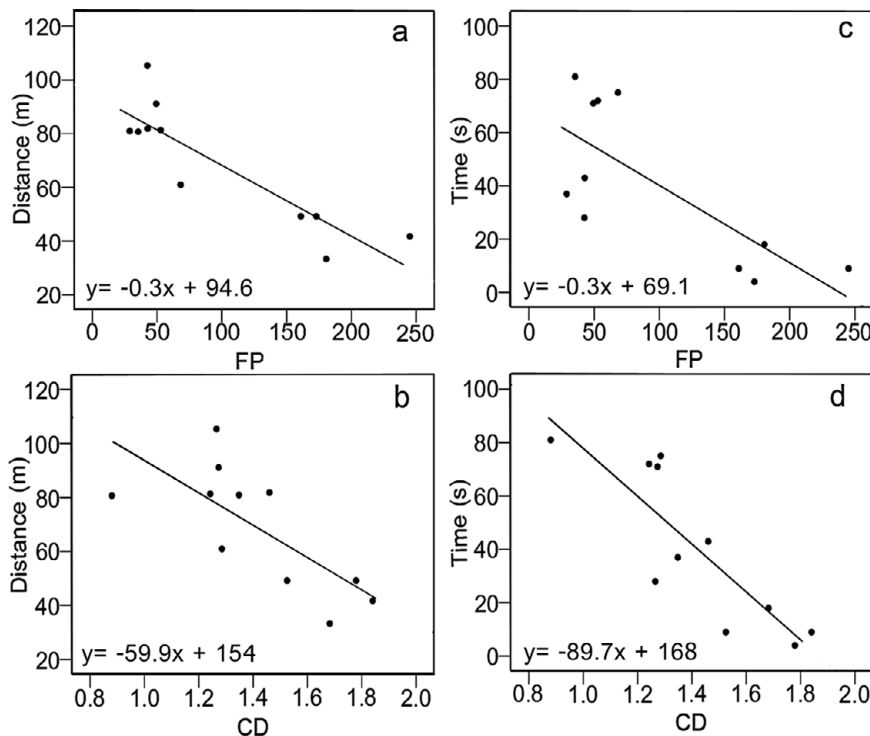## Distances moved between fruiting trees in relation to available fruit resources

Distances moved between fruiting trees also varied notably by month. October was the month with the longest distances moved between fruiting trees and May distances were shortest (Table 1). For only one out of the 10 groups was there a significant correlation between distance moved between fruit trees and fruit productivity ($r_s = -0.80$, $P = 0.003$) and there was no trend for the remaining nine groups (r_s was < 0 for five of the 10 groups). However, when the data were pooled, distance

Table 1. Distance (mean ± SD) moved between fruiting trees (m), feeding time on a fruiting tree (s), feeding range (ha h^{-1}), percentage of average home range covered and total distance moved (m h^{-1}) by puff-throated bulbuls during 4 h mo^{-1} of observation for 10 bulbul family groups.

Month	Distance moved (m)	Feeding time budget (s)	Feeding range (ha h^{-1})	% of average home range	Total distance moved (m h^{-1})
May	33 ± 13	18 ± 13	0.13 ± 0.05	15.2	307 ± 137
June	42 ± 22	9 ± 9	0.11 ± 0.04	14.7	224 ± 76
July	49 ± 28	9 ± 6	0.17 ± 0.05	19.4	368 ± 240
August	49 ± 21	4 ± 7	0.10 ± 0.07	12.3	123 ± 98
September	–	–	–	–	–
October	105 ± 79	28 ± 14	0.13 ± 0.07	14.2	127 ± 48
November	61 ± 33	75 ± 34	0.19 ± 0.06	21.8	247 ± 61
December	81 ± 37	81 ± 50	0.16 ± 0.06	19.8	206 ± 54
January	81 ± 40	37 ± 44	0.16 ± 0.04	20.7	200 ± 42
February	82 ± 38	43 ± 29	0.24 ± 0.11	27.7	305 ± 67
March	81 ± 21	72 ± 39	0.20 ± 0.08	25.6	254 ± 62
April	91 ± 16	71 ± 37	0.16 ± 0.04	20.5	256 ± 67
	69 ± 23	41 ± 25	0.16 ± 0.03	18.9	238 ± 74

moved between fruiting trees and fruit productivity were negatively correlated (r_s = −0.76, P = 0.006) (Figure 3). For distance moved between fruiting trees in relation to the coefficient of dispersion, eight groups out of 10 had trends in the same direction. Furthermore, when data from all 10 bulbul groups were pooled monthly, there was also a clear and significant negative correlation between distances moved between fruiting trees and coefficient of

dispersion (r_s = −0.64, P = 0.01) (Figure 3). Bulbuls moved further between subsequent feeding trees when food was scarce, and when it was more dispersed. The average (± SD) total distance travelled by puff-throated bulbul per observation period ranged from 123 ± 98 m h^{-1} (August) to 368 ± 240 m h^{-1} (July), with an average total distance of 238 ± 74 m h^{-1} for the study period (Table 1). There was no significant correlation between

Figure 3. Relationship between the average distances moved by *Alophoixus pallidus* between fruiting trees and fruit productivity (FP) (r_s = −0.76, P = 0.007) (a), and coefficient of dispersion of fruiting trees/lianas (CD) (r_s = −0.64, P = 0.04) (b). Relationship between the average time spent in a fruiting tree (s) and total FP (r_s = −0.52, P = 0.09) (c) and CD (r_s = −0.72, P = 0.01) (d). The 11 points represent monthly average distances and times derived from 10 *A. pallidus* groups during 11 mo of observations. Lines of best fit were shown for illustration.

total distance moved and fruit productivity ($r_s = 0.30$, $P = 0.37$) or the coefficient of dispersion ($r_s = 0.12$, $P = 0.71$) using all groups combined. There was also no correlation between the median total distance moved and median distance moved between fruiting trees ($r_s = 0.37$, $P = 0.26$) or median total distance moved and median time spent on a fruiting tree ($r_s = 0.11$, $P = 0.75$) also based on all groups combined.

Foraging time in relation to fruit resources

There was large variation in the time a particular group foraged on a fruiting tree ranging from 1 to 219 s. The average time spent on a fruiting tree also varied throughout the study period. August was the month in which the puff-throated bulbul spent the shortest time on the fruiting trees after which time spent increased to December, which was the month with the longest time spent on fruiting trees (Table 1). Two of the 10 focal groups had significant negative correlations between foraging time on a fruiting tree and fruit productivity ($r_s = -0.80$, $P = 0.003$ and $r_s = 0.79$, $P = 0.003$); six of the remaining eight groups also had trends in the same direction, although correlations were not significant. The data from all groups combined also indicated that there was a negative correlation between time spent on fruiting trees and fruit productivity ($r_s = -0.58$, $P = 0.05$). Two of the 10 groups had significant negative correlations between foraging time on a fruiting tree and the coefficient of dispersion ($r_s = -0.81$, $P = 0.002$ and $r_s = -0.76$, $P = 0.006$). Again six of the remaining eight groups also had trends in the same direction. The pooled data also demonstrated that time spent was also significantly negatively correlated with the coefficient of dispersion ($r_s = -0.83$, $P = 0.001$) (Figure 3). There was a significant positive correlation between the median time spent on a particular fruiting tree and the median distance moved between fruiting trees also based on the pooled data ($r_s = 0.70$, $P = 0.016$).

Examination of the mean distance, feeding range and foraging time in relation to season, found no significant differences between the breeding and the non-breeding season (t-test: $t_{distance} = -0.88$, $df = 9$, $P = 0.40$; $t_{range} = 0.80$, $df = 9$, $P = 0.44$; $t_{time} = -0.43$, $df = 9$, $P = 0.68$, respectively).

DISCUSSION

There was clear seasonal fluctuation in fruit productivity on the plot, which appeared to be correlated with rainfall. Trees tended to produce more fruits in the wet season relative to the dry season. A large drop in fruit productivity was detected between August and October at the end of the wet season. This reduction was primarily attributed to the general cycle of plants known to comprise the diet of *A. pallidus* and the rapid disappearance of fruits from a large number of *Symplocos cochinchinensis* (Symplocaceae) trees, a species which is known to vary considerably in productivity among years (Brockelman *et al.* in press). These changes were significantly correlated with both the time birds spent on, and how far they travelled between, fruiting trees.

Effect of fruit resources on feeding range

The total range of these territorial *A. pallidus* groups did not appear to be related to fruit productivity or the dispersion of fruit resources. This and previous work suggested that bulbul territory size fluctuates little with the exception of temporary increases for groups with fledged young (Tanasarnpaiboon, unpubl. data). This contrasts with studies of other tropical birds (Holbrook & Smith 2000, Tremblay *et al.* 2005), which report changes in feeding ranges or home ranges associated with food availability, although all of these species were non-territorial. As most tropical frugivorous birds examined to date appear to be non-territorial (Stutchbury & Morton 2001), the differences observed here may be due to our study species having small (~2.2 ha) territories resulting in the frequent re-use of the same fruiting trees within short periods of time. Thus, while during certain months of lower fruit availability cumulative foraging distances travelled per unit time were relatively high, the total foraging area remained relatively small.

Distances moved between fruit foraging locations

Alophoixus pallidus groups moved longer distances between fruiting trees when fruit abundance was lower and fruit dispersion higher as demonstrated in other studies (Holbrook & Smith 2000, Korine *et al.* 2000). As observed in studies in tropical Central America, there was a significant negative correlation between dispersion of fruiting trees/lianas and foraging distance, whereby birds flew shorter distances as fruit resources became more aggregated (Korine *et al.* 2000, Tremblay *et al.* 2005).

Mean distances moved between feeding locations of *A. pallidus* (69 m) appeared to be roughly similar to three species of frugivorous bird of somewhat smaller body size (20–33 g vs 37 g for *A. pallidus*) studied in neotropical forests (57 m) (Murray 1988). The only other movement data available near our study area were for the much larger great hornbill (*Buceros bicornis*) (2150–4000 g) which had long average daily movements of approximately 7600 m (Poonswad & Tsuji 1994). In general however, broad interspecific differences in

distances moved are likely to be related to body size (Westcott & Graham 2000) and to some extent predation risk (Oppel & Mack 2010). Murray (1988) also noted that movement patterns of frugivorous birds in his neotropical study area also shifted with changes in the dispersion of fruiting trees as we found in our study, however Murray (1988) did not explicitly map fruit resources.

There was no correlation between either fruit availability or dispersion of fruiting trees/lianas with the total distance moved per unit time. This contradicts findings reported in Costa Rican rain forest where frugivorous birds used a different tactic, moving into different habitat when the resources in the primary forest declined (Levey 1988). *Alophoixus pallidus* is territorial year round; groups travel around their home range for reasons other than foraging, particularly territorial defence which is likely a significant determinant of total movement per unit time (Schoener 1968).

Foraging time in relation to resources

Alophoixus pallidus tended to feed longer in a particular fruiting tree when fruit was in lower abundance and more widely dispersed as observed in other systems (Morales & Carlo 2006). Spending more time in a given fruit tree or resource may maximize energy gain before moving to the next fruiting tree although there appears to be a trade-off with predation risk (Oppel & Mack 2010). Even if a resource has low availability but the cost of leaving is higher, foragers will tend to stay with the same resource longer (Stephens & Krebs 1986). Although few data on mean residence times in fruiting trees for other bulbuls exist, *A. pallidus* spent relatively less time on a particular fruiting tree when compared with other bulbuls, 41 s (this study) vs 150 s (Weir & Corlett 2006), or other passerines in the region (60–600 s) (Oppel & Mack 2010). While this may also be partly a function of crop size and other factors such as predation pressure (Oppel & Mack 2010, Weir & Corlett 2006), it is possible that some of the difference in time spent feeding reflects the abundance and distribution of resources between closed-canopy forest and open grassland with scattered trees of Weir & Corlett (2006). Mean visiting times to fruiting trees of frugivorous birds from neotropical montane forest also suggest notably longer visitations (420–720 s) (Murray 1988) compared even with the longest recorded visiting time of *A. pallidus* (219 s). Again, differences in movement patterns are likely the result of multiple factors (Murray 1988, Oppel & Mack 2010, Weir & Corlett 2006, Westcott & Graham 2000) and it is currently unknown which of the various factors are responsible for such regional differences.

Although *A. pallidus* is unusual in that it is a cooperative breeder, and as such may have somewhat different foraging patterns than non-cooperative breeders, this study provides an initial quantitative assessment of the movement patterns of a forest-dwelling bulbul indicating that: (1) its movement patterns are highly correlated with food availability and (2) this bulbul and probably many other similarly sized frugivores from tropical Asia and other regions move longer distances with longer residence times in fruiting trees when fruit availability is low and widely dispersed even taking into account baseline differences in distances travelled or residence times. Such trends also strongly suggest that models of seed disperser behaviour need to account for the dynamics of fruit availability.

LITERATURE CITED

AU, A. Y. Y., CORLETT, R. T. & HAU, B. C. H. 2006. Seed rain into upland plant communities in Hong Kong, China. *Plant Ecology* 186:13–22.

BOITANI, L. & FULLER, T. K. 2000. *Research techniques in animal ecology.* Columbia University Press, New York. 442 pp.

BROCKELMAN, W. Y. 1998. Long term ecological research plot for the study of animal diets in Khao Yai National Park. Pp. 307–310 in Poonswad, P. (ed.). *The Asian hornbills: ecology and conservation.* Thai Studies in Biodiversity, No. 2. Biodiversity Research and Training Program, Bangkok.

BROCKELMAN, W. Y., NATHALANG, A. & GALE, G. A. in press. The Mo Singto forest dynamics plot, Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society* 57:35–55.

CHAPMAN, C. A., CHAPMAN, L. J., WRANGHAM, R., HUNT, K., GEBO, D. & GARDNER, L. 1992. Estimates of fruit abundance of tropical trees. *Biotropica* 24:527–531.

CHAPMAN, C. A., WRANGHAM, R. & CHAPMAN, L. J. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology* 36:59–70.

CORLETT, R. T. 1998. Frugivory and seed dispersal by vertebrates in the Oriental (Indomalayan) Region. *Biological Reviews* 73:413–443.

CORLETT, R. T. 2009. *The ecology of tropical East Asia.* (First edition). Oxford University Press, Oxford. 272 pp.

FOGDEN, M. P. L. 1972. The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis* 114:307–343.

GALE, G. A., ROUND, P. D., PIERCE, A. J., NIMNUAN, S., PATTANAVIBOOL, A. & BROCKELMAN, W. Y. 2009. A field test of distance sampling methods for a tropical forest bird community. *The Auk* 126:439–448.

GERWING, J. J., SCHNITZER, S. A., BURNHAM, R. J., BONGERS, F., CHAVE, J., DEWALT, S. J., EWANGO, C. E. N., FOSTER, R., KENFACK, D., MARTINEZ-RAMOS, M., PARREN, M., PARTHASARATHY, N., PEREZ-SALICRUP, D. R., PUTZ, F. E. & THOMAS, D. W. 2006. A standard protocol for liana censuses. *Biotropica* 38:256–261.

HERRERA, C. M. 2002. Seed dispersal by vertebrates. Pp. 185–208 in Herrera, C. M. & Pellmyr, O. (eds.). *Plant–animal interactions: an evolutionary approach*. Blackwell, Malden.

HOLBROOK, K. M. & SMITH, T. B. 2000. Seed dispersal and movement pattern in two species of *Ceratogymna* hornbill in a West Africa lowland forest. *Oecologia* 125:249–257.

HOPPES, W. G. 1987. Pre-and post-foraging movements of frugivorous birds in an eastern deciduous forest woodland, USA. *Oikos* 49:281–290.

KARUBIAN, J. & DURAES, R. 2009. Effects of seed disperser social behaviour on patterns of seed movement and deposition. *Oecologia Brasiliensis* 13:45–57.

KITAMURA, K., YUMOTO, T., POONSWAD, P., CHUALUA, P., PLONGMAI, K., MARUHASHI, T. & NOMA, N. 2002. Interaction between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133:559–572.

KITAMURA, K., YUMOTO, T., POONSWAD, P., CHUALUA, P. & PLONGMAI, K. 2004. Characteristics of hornbill-dispersed fruits in a tropical seasonal forest in Thailand. *Bird Conservation International* 14:81–88.

KORINE, C., KALKO, E. K. V. & HERRE, E. A. 2000. Fruit characteristics and factors affecting fruit removal in a Panamanian community of strangler figs. *Oecologia* 123:560–568.

LEKAGUL, B. & ROUND, P. D. 1991. *A guide to the birds of Thailand*. Saha Karn Bhaet, Bangkok. 457 pp.

LEVEY, D. J. 1987. Seed size and fruit-handling techniques of avian frugivore. *American Naturalist* 129:471–485.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating abundance. *Ecological Monographs* 58:251–269.

MCCLURE, H. E. 1974. Some bionomics of the birds of Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society* 25:99–184.

MORALES, J. M. & CARLO, T. A. 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology* 87:1489–1496.

MURRAY, G. M. 1988. Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs* 58:271–298.

NIMNUAN, S., ROUND, P. D. & GALE, G. A. 2004. Structure and composition of mixed-species insectivorous bird flocks in Khao Yai National Park, Thailand. *Natural History Bulletin of the Siam Society* 52:71–79.

OPPEL, S. & MACK, A. L. 2010. Bird assemblage and visitation pattern at fruiting *Elmerrillia tsiampaca* (Magnoliaceae) trees in Papua New Guinea. *Biotropica* 42:229–235.

PIERCE, A. J., TOKUE, K., POBPRASERT, K. & ROUND, P. D. 2004. Observations on the breeding of the puff-throated bulbul *Alophoixus pallidus* in north-east Thailand. *Forktail* 20;100–101.

POONSWAD, P. & TSUJI, A. 1994. Ranges of males of the Great Hornbill *Buceros bicornis*, Brown Hornbill *Ptilolaemus tickelli* and Wreathed Hornbill *Rhyticeros undulatus* in Khao Yai National Park, Thailand. *Ibis* 136:79–86.

RAGUSA-NETTO, J. 2002. Fruiting phenology and consumption by birds in *Ficus calyptroceras* (Miq.) Miq. (Moraceae). *Brazilian Journal of Biology* 62:339–346.

ROBSON, C. 2000. *Field guide to the birds of Thailand and South-East Asia*. Asia Books, Bangkok. 272 pp.

SANKAMETHAWEE, S., PIERCE, A. J., GALE, G. A. & HARDESTY, B. D. 2011. Plant–frugivore interactions in an intact tropical forest in northeast Thailand. *Integrative Zoology* 6:195–211.

SANKAMETHAWEE, W., GALE, G. A. & HARDESTY, B. D. 2009. Post-fledging survival of the cooperatively breeding puff-throated bulbul (*Alophoixus pallidus*). *Condor* 111:675–683.

SAVINI, T., BOESCH, C. & RICHARD, U. 2008. Home-range characteristics and the influence of seasonality on female reproduction in White-handed gibbon (*Hylobateslar*) at KhaoYai Nation Park, Thailand. *American Journal of Physical Anthropology* 135:1–12.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. *Ecology* 49:123–139.

STEPHENS, D. W. & KREBS, J. R. 1986. *Foraging theory*. Princeton University Press, Princeton. 250 pp.

STUTCHBURY, B. J. M. & MORTON, E. S. 2001. *Behavioral ecology of tropical birds*. (First edition). Academic Press, San Diego. 165 pp.

TREMBLAY, I., THOMAS, D., BLONDEL, J., PERRET, P. & LAMBRECHTS, M. M. 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican blue tits *Parus caeruleus*. *Ibis* 147:17–24.

WEIR, J. E. S. & CORLETT, R. T. 2006. How far do birds disperse seeds in the degraded tropical landscape of Hong Kong, China? *Landscape Ecology* 22:131–140.

WENNY, D. G. & LEVY, D. J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences USA* 95:6204–6207.

WESTCOTT, D. A. & GRAHAM, D. L. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* 122:249–257.

WHEELWRIGHT, N. T. 1991. How long do fruit-eating birds stay in the plants where they feed? *Biotropica* 23;29–41.

Appendix 1. The top five fruit species consumed mo^{-1} by puff-throated bulbul during the study period (n observations h^{-1}). Zero indicates that no consumption of the particular species was observed.

Species	Habit	Family	M	J	J	A	S	O	N	D	J	F	M	A	Mean
Aidia densifolia (Wall.) Masam.	Tree	Rubiaceae	0	0	1.5	0	0	0.5	0.8	0.8	1	0.3	0	0	0.4
Alangium kurzii Craib	Tree	Alangiaceae	0	0	0.3	0	0	0	0	0	0	0	0	0	0.03
Ardisia colorata Roxb.	Tree	Myrsinaceae	0.5	0.3	0.5	0	0	0	0	0	0.3	0	0	3.8	0.5
Ardisia nervosa Flet.	Tree	Myrsinaceae	0	0	0	0	0	0	0	0	0	0.3	0	0	0.0
Bridelia insulana Hance	Tree	Euphorbiaceae	0	0	0	0	0	0	0	0	0	0.3	0.3	3	0.3
Cinnamomum subavenium Miq.	Tree	Lauraceae	0	0	0	0	0	0	0	0	0.5	1.3	0	0	0.2
Dendrocnide stimulans (L.f.) Chew	Tree	Urticaceae	0	0	0	0	0	1	0	0	0	0	0	0	0.1
Eurya nitida Korth. var. *siamensis* (Craib) H. Keng	Tree	Theaceae	1	0	0.8	0	0	0	0	0	1	0	0.5	0.3	0.3
Ficus altissima Bl.	Tree	Moraceae	0	0	0.5	0	0	0	0	0	0.3	0	0.5	0.3	0.1
Ficus fistulosa Reinw. ex Bl. var. *fistulosa*	Tree	Moraceae	0	0	0	0	0	0	0	0	0.3	0.3	0.3	0	0.1
Ficus glaberrima Bl. var. *glaberrima*	Tree	Moraceae	0	0	0	0	0	0	0	0	0.3	0.3	0	0	0.1
Ficus nervosa Hey. ex Roxb. ssp. *nervosa*	Tree	Moraceae	0	0	0	0	0	0	0	0	0	0.3	0	0	0.0
Gironniera nervosa Planch.	Tree	Ulmaceae	3	2.5	3	5.3	0	2.5	3	6.3	2.5	7.5	7	8.3	4.2
Ilex chevalieri Trad.	Tree	Aquifoliaceae	0.3	0	0	0	0	1.3	0	0	0	0	0	0	0.1
Litsea verticillata Hance	Tree	Lauraceae	0	0	0	0	0	0	0	0.5	0.3	0	0	0	0.1
Canthium glabrum Bl.	Tree	Rubiaceae	0	0	0	0	0	0	0	0	0	0	0.5	0	0.04
Polyosma elongata Geddes	Tree	Escalloniaceae	0	0	0	0	0	0	0.8	0	0	0	0	0	0.1
Prunus arborea (Bl.) Kalk. var. *montana* (Hk.f.) Kalk.	Tree	Rosaceae	0	0	0	0	0	0	1	0.8	0	1	0	0	0.2
Schefflera heptaphylla (L.) Frodin	Tree	Araliaceae	0	0	0	0	0	0	0.3	5	1.8	0.3	0	0	0.6
Symplocos cochinchinensis (Lour.) S. Moore	Tree	Symplocaceae	6.5	1.5	1	0	0	0	0	0	0.3	0.3	0	0	0.8
Celastrus monospermus Roxb.	Liana	Celastraceae	0	0	0	0	0	0	0	0	0	0.8	0	0	0.1
Desmos dumosus (Roxb.) Saff. var. *glabrior* Craib	Liana	Annonaceae	0	0	0	0	0	0	0	0	2	0.8	1	0	0.3
Dissochaeta divaricata G. Don	Liana	Melastomataceae	0.8	2.5	0.5	1.5	0	0	1	0.5	0.3	0	0	0.5	0.6
Ficus sagitatta Vahl var. *sagittata*	Liana	Moraceae	0	0	0	0	0	0	0	0	0.5	0.3	0.3	0	0.1
Ficus villosa Bl.	Liana	Moraceae	0	0	0	0	0	0	0	0	0.3	0.8	2.5	0	0.3
Morinda umbellata L.	Liana	Rubiaceae	0	0	0.8	0.8	0	0	0	0	0	0	0	0	0.1
Oxyceros longifora (Lmk.) Yama.	Liana	Rubiaceae	0	0.3	0	0	0	0	0.8	1.8	1.5	0.3	0	0	0.4
Phyllanthus reticulatus Poir.	Liana	Euphorbiaceae	0.3	0	0.3	0	0	0	0.8	0	0.5	0	1.3	2.3	0.5
Piper retrofractum Vahl	Liana	Piperaceae	0	0	0	0	0	0.3	0	0	1	1.8	1.5	3	0.6
Piper ribesoides Wall.	Liana	Piperaceae	2.8	0	0	0	0	0	0	0	0	0	0	3	0.5
Poikilospermum suaveolens (Lour.) Merr.	Liana	Urticaceae	0	0	0	0	0	0	0	0	0	0	0.3	0	0.03
Schefflera elliptica (Bl.) Harms	Liana	Araliaceae	0	0	0	1.5	0	0	0	0	0	0	0	0	0.1
Tetrastigma laoticum Gagnep.	Liana	Vitaceae	0	0	0	0	0	1.3	0.3	0.3	0	0.3	0	0	0.2
Tetrastigma aff. *pyriforme* Gagnep.	Liana	Vitaceae	0	0	0	0	0	1.3	0.3	0.3	0	0.3	0	0	0.2