

RESEARCH

Open Access



Body-size dependent foraging strategies in the Christmas Island flying-fox: implications for seed and pollen dispersal within a threatened island ecosystem

Christopher M. Todd^{1*} , David A. Westcott^{2,3}, John M. Martin⁴, Karrie Rose⁴, Adam McKeown⁵, Jane Hall⁴ and Justin A. Welbergen¹

Abstract

Background: Animals are important vectors for the dispersal of a wide variety of plant species, and thus play a key role in maintaining the health and biodiversity of natural ecosystems. On oceanic islands, flying-foxes are often the only seed dispersers or pollinators. However, many flying-fox populations are currently in decline, particularly those of insular species, and this has consequences for the ecological services they provide. Knowledge of the drivers and the scale of flying-fox movements is important in determining the ecological roles that flying-foxes play on islands. This information is also useful for understanding the potential long-term consequences for forest dynamics resulting from population declines or extinction, and so can aid in the development of evidence-based ecological management strategies. To these ends, we examined the foraging movements, floral resource use, and social interactions of the Critically Endangered Christmas Island flying-fox (*Pteropus natalis*).

Methods: Utilization distributions, using movement-based kernel estimates (MBKE) were generated to determine nightly foraging movements of GPS-tracked *P. natalis* ($n = 24$). Generalized linear models (GLMs), linear mixed-effect models (LMMs), and Generalized linear mixed-effects model (GLMMs) were constructed to explain how intrinsic factors (body mass, skeletal size, and sex) affected the extent of foraging movements. In addition, we identified pollen collected from facial and body swabs of *P. natalis* ($n = 216$) to determine foraging resource use. Direct observations ($n = 272$) of foraging *P. natalis* enabled us to assess the various behaviors used to defend foraging resources.

Results: Larger *P. natalis* individuals spent more time foraging and less time traveling between foraging patches, traveled shorter nightly distances, and had smaller overall foraging ranges than smaller conspecifics. Additionally, larger individuals visited a lower diversity of floral resources.

Conclusions: Our findings suggest that smaller *P. natalis* individuals are the primary vectors of long-distance dispersal of pollen and digested seeds in this species, providing a vital mechanism for maintaining the flow of plant genetic diversity across Christmas Island. Overall, our study highlights the need for more holistic research approaches that incorporate population demographics when assessing a species' ecological services.

*Correspondence: Cmtodd@hawaii.edu

¹ The Hawkesbury Institute for the Environment, Western Sydney

University, Richmond, NSW 2753, Australia

Full list of author information is available at the end of the article



© The Author(s) 2022. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

Keywords: Bats, Ecosystem services, Foraging range, Fruit bats, GPS telemetry, Pollination, Pteropodidae, *Pteropus natalis*

Background

Animal-mediated pollination and seed dispersal are fundamental to shaping the ecological and evolutionary processes that affect biodiversity and help maintain ecosystem health. Over ecological timeframes, dispersal methods and patterns influence where individual plants are deposited, their prospects for survival, and ecosystem-wide population dynamics through effects on immigration, emigration and survival [37]. Over evolutionary timeframes, dispersal patterns determine both gene flow between populations and the frequency with which a species experiences new selection regimes that facilitate evolution in novel environments [73]. Among plants that are dispersed by animals, gene-flow through seed dispersal and pollination are affected by various characteristics of a dispersers' biology such as population density, food availability, and behavior [43, 46]. Despite the recognized importance of the dispersal services provided by animals, the processes that influence seed and pollen dispersal are not fully understood. How an animal's behavior affects its foraging patterns and movements, and therefore its dispersal of seeds and pollination of flowers, is of particular interest among conservation biologists. This knowledge can be incorporated into models estimating dispersal patterns [88] and assess the importance of the dispersers' ecological functions. Together this information can be used to predict how anthropogenic disruptions to the dispersal agent may affect the maintenance of diversity and ecosystem health [58].

Foraging movements and associated pollination and seed dispersal services have been shown to vary within species due to a variety of factors [29, 94]. In general, within and between species, larger individuals have a greater capacity to move larger distances than smaller individuals [18, 66, 68]. However, larger individuals also have greater energy demands and a range of behaviors have been documented to secure this energy, including increased foraging area [45, 54]. Social interactions, such as those involved in resource defense can also influence the foraging space of individuals, and so limit or increase the quantity of seed and pollen moved by a given dispersal agent [42]. If an individual is successful at monopolizing a stable resource, the number of other foraging sites it visits is likely to decrease and the quality of its dispersal service is likely to be reduced [42]. Conversely, the foraging interference caused to competitors by a territorial individual may increase the dispersal distances provided by the competitors by forcing them away from

the fruiting or flowering tree [44, 46, 53, 71]. In many systems, resource defense is mediated by body size-dependent dominance characteristics [5, 20, 72], with larger more dominant individuals tending to be sedentary while defending the richest resources, and smaller individuals being forced to seek out more marginal habitats [17, 38]. Thus, while larger individuals can have greater capacities to move larger distances, competitive interactions at foraging sites can cause the movements and dispersal services of larger individuals to be more localized than those of smaller individuals.

Flying-foxes of the family Pteropodidae are the world's largest flying mammals, and provide critical ecological services [4], aided by the taxons' extreme mobility among foraging and roosting areas [13, 31, 86]. As both pollinators and seed dispersers, flying-foxes are vitally important for the preservation and regeneration of forests, especially on islands that have evolved with depauperate pollinator and seed disperser guilds [25, 30]. Throughout the Pacific, flying-foxes are known to visit at least 92 genera of plants in 50 different families [23, 51]. On some islands, flying-foxes are responsible for 80–100% of the seed rain [25]. However, it has been suggested that the effectiveness of flying-foxes as vectors for plant dispersal is strongly dependent on the their population densities [53], which is of serious conservation concern as many insular flying-fox species are in decline [56, 57].

In flying-foxes, larger, older and more experienced individuals defend territories and displace subordinates from foraging areas [22, 52, 71, 87] using a variety of mechanisms including threatening vocalizations and threatening gestures such as wing spreading or clapping, and chases, fighting and aerial pursuit [14, 60, 71, 81, 89, 90]. When the abundance of flying-foxes declines, resource defense interactions become less common, and so flying-foxes may become functionally extinct, ceasing to be effective dispersal agents long before becoming rare [53]. The reduction and loss of insular flying-fox species exacerbates the vulnerability of island endemic plants that are dependent on a limited suite of pollinators and seed dispersers [24, 25], and so it is important to understand the ecological roles that different-sized individuals have as seed and pollen dispersal agents on islands.

The Christmas Island flying-fox (*Pteropus natalis*) is a medium-sized species of flying-fox limited to Christmas Island in the Indian Ocean, where it is considered to perform critical pollen and seed dispersal services for a broad suite of native plants [39, 80]. It is the only

remaining native mammal on Christmas Island [2, 34, 91] following the extinctions during the twentieth century of the Christmas Island rat (*Rattus macleari*), the bulldog rat (*Rattus nativitatis*), the Christmas Island shrew (*Crocidura trichura*), and the extinction of the Christmas Island pipistrelle (*Pipistrellus murrayi*) in 2009 [47]. *Pteropus natalis* has recently undergone a 50 – 75% population decline [64] so that the species is now listed as Critically Endangered under Australian federal legislation [27]. The cause of its decline is not fully understood, which is of serious concern for the conservation of this species and the floral species it services within a small insular ecosystem. *Pteropus natalis* is known to forage on the pollen and fruits of at least 51 species of plants (23 native, 28 introduced) (Additional file 1: Table S1) from 44 genera and 31 families (personal observations, [39, 80]). Several of the endemic plant species are thought to be “chiropterophilous” [39, 80] as they are characterized by large, odorous, nectar rich flowers that open at night [69], further highlighting the important and unique ecological role that *P. natalis* plays as a vector for plant dispersal on Christmas Island.

In this study we examine the foraging ecology of *P. natalis*. Specifically, we document *P. natalis*' foraging movements and diet, and describe their agonistic interactions at foraging sites. Based on our observations and the literature, we predict that larger individuals will i) visit fewer foraging sites, ii) move less frequently between foraging sites, and as a consequence of this, iii) forage on fewer plant species. We consider our findings in light of alternative explanations of how body size may affect foraging movement dynamics, and discuss the implications for the ecological roles that different-sized flying-foxes have as seed and pollen dispersal agents on islands.

Methods

Study location

Christmas Island is a small, 135 km², geographically isolated island in the Indian Ocean, located approximately 380 km south of Java, Indonesia, located at 10° 25' S and 105° 40' E. It is monsoonal with distinct wet (November–June) and dry (July–October) seasons. The vegetation on Christmas Island has been categorized into seven main types: evergreen forest, semi-deciduous forest, deciduous scrub, perennial wetland forest, coastal fringe, rehabilitation, regrowth and weed dominated, and pioneer growth (see Additional file 1: Table S2 for further classification and habitat description).

Data collection

Capture and body measurements

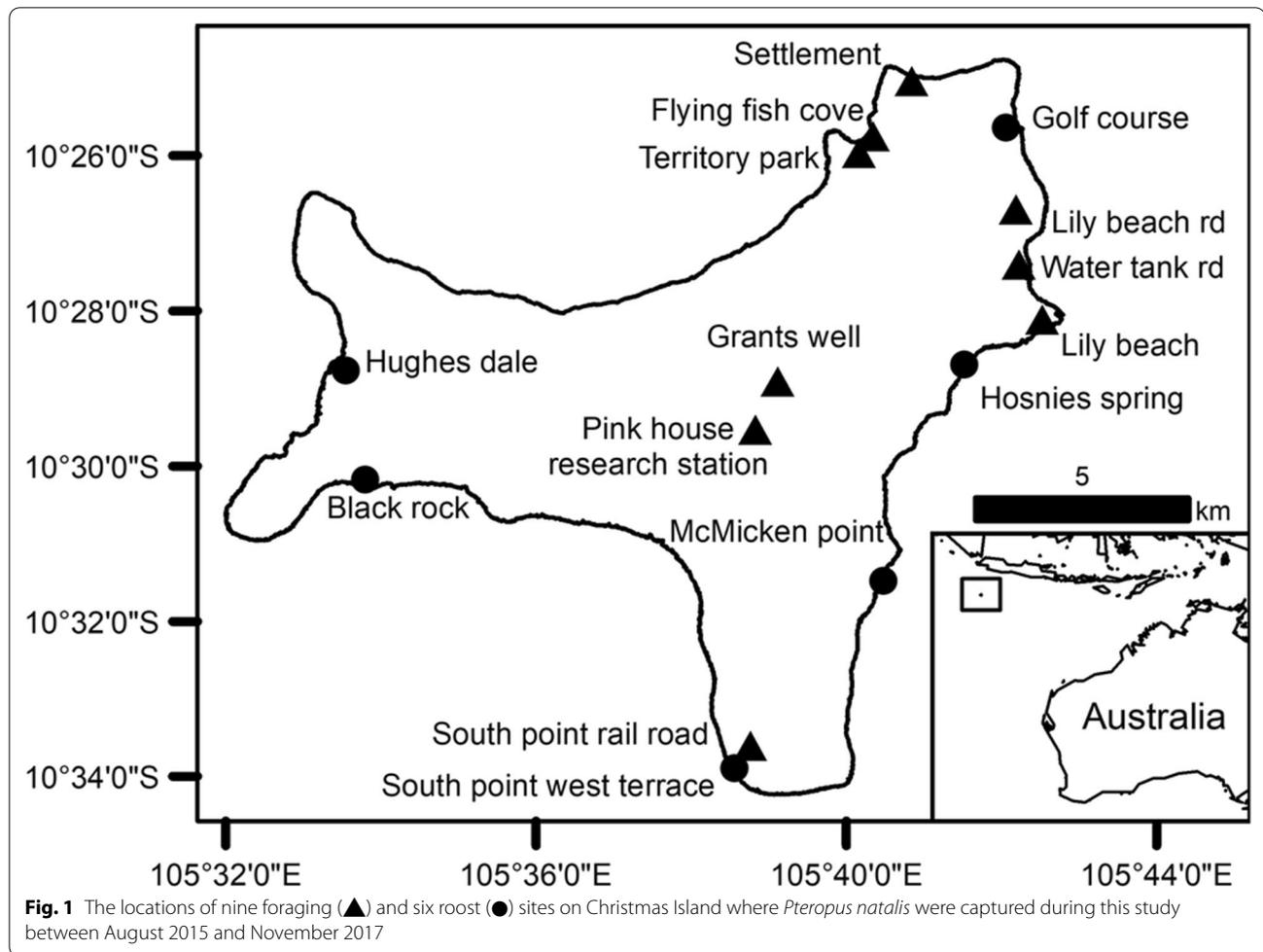
Pteropus natalis were caught at foraging and roost sites across Christmas Island (Fig. 1) between August 2015

and November 2017 using 3.2 × 12 m nylon mist nets with a 45 × 45 mm mesh size (Ecotone; Gdynia, Poland) or an aluminum anglers' landing net with a 64 × 56 cm hoop dimension mounted on an 8 m pole. Flying-foxes were weighed to the nearest 1 g using a 5-kg digital scale (Breville, Sydney, New South Wales, Australia). Forearm length, thumb length, thumb claw length, and tibia length were measured to the nearest 0.1 mm with calipers (Just Tools, Melbourne, Victoria, Australia).

Pollen collection and identification

Pollen was collected from captured *P. natalis* by swabbing a cotton ball once across the face, body, and both sides of the wings. Pollen samples were then stored in 90% ethanol. Pollen samples ($n=216$) were collected from individuals captured between 1400 and 0730 h. The greatest proportion (50%) of pollen samples was collected from individuals captured between 1700 and 2100 h (see Additional file 1: Figure S1). We removed samples ($n=46$) collected between the months January to June (a period when flowering is at its lowest) because they did not contain any pollen. We also removed samples ($n=55$) containing pollen loads < 20 total pollen grains, that were substantially lower the mean pollen load ($\bar{x}=150.89$). Neither the time of capture nor nightly rainfall was a significant factor in the presence or absence of pollen among the collected samples (GLMM; time of capture: $Z_{4,216}=0.32$, $P=0.751$; rainfall: $Z_{4,216}=-1.62$, $P=0.105$).

To better understand the foraging resources used by *P. natalis* we identified the pollen collected from facial and body swabs among the broader population ($n=115$). At the time of capture, a cotton ball wiped over the face, wings and fur of an individual animal was saturated in ethanol until processing. To extract the pollen samples, the cotton ball was placed into a 300 ml glass beaker with 40 ml of deionized water and then placed into an ultrasonic bath and agitated for several minutes to remove the pollen from the cotton. The cotton was removed and 5–6 drops of 1% Safranin stain solution (Thermo Fisher Scientific Pty Ltd, Waltham, Massachusetts, United States) was placed into the pollen suspension. A portion of the pollen suspension was then placed in a 10 mL conical centrifuge tube and centrifuged at 3000 RPM for 3 min. The supernatant was decanted without disturbing the pollen collection at the bottom of the tube. The pollen pellet was then resuspended using a vortex mixer and the centrifuge tube was refilled with remaining pollen suspension and placed back in the centrifuge. This process was repeated until all of the pollen suspension had been centrifuged and poured off leaving a single pollen pellet in the conical tube. A glass Pasteur pipette was used to extract the pollen pellet and place it into a glass vial with



glycerol for storage. A 20 μ l aliquot of the pollen/glycerol mixture was placed onto a glass slide, covered with a 22 \times 40 mm coverslip, and sealed with lacquer. Pollen was viewed at 400 \times magnification using a Zeiss Axio Imager 1 microscope (Carl Zeiss Microscopy Pty Ltd, Jena, Germany) and identified to genus level, and species level where possible, using The Australia National University Australasian Pollen and Spore Atlas (<http://apsa.anu.edu.au>) and reference samples collected on Christmas Island. While the different pollen types all represent distinct species, we use the term “pollen type” to account for the fact that a small proportion of pollen types could not be formally classified to species level. Three transects were made across the length of each slide, counting the numbers of each pollen type identified.

GPS telemetry

We deployed solar-powered Camazotz GPS telemetry nodes [41], hereafter “GPS nodes”, on 24 of the caught flying-foxes (16 males, 8 females; Additional file 1:

Table S3). Each GPS node was 5 \times 3 \times 1.5 cm, plus a 6 cm antenna. GPS nodes were fixed with metal rivets to a collar that consisted of a 117 \times 7.5 \times 1 mm piece of leather sewn to a 110 \times 15 \times 2 mm piece of neoprene. A 3.75 mm neoprene overlap was allowed on the linear sides of the leather to avoid it contacting the skin and causing discomfort for the flying-fox. The collar, with the attached GPS node, was trimmed to fit individual flying-foxes and secured using monofilament polyglyconate absorbable sutures (Covidien, Dublin, Ireland). Sutures were placed at the top and bottom of the overlapping piece of leather. To aid in the relocation of the tagged flying-fox we attached a 1 g VHF transmitter (ATS Telemetry, Isanti, Minnesota, United States) to the leather of the collar next to the GPS node. The combined weight of the GPS node, VHF transmitter, and collar was 19 g; less than 5% of each animal’s body mass.

We tracked the 24 individuals (16 male and 8 female) for 3–28 consecutive nights (1600–0600 h), recording a total of 5992 positions over 253 bat nights (Additional

file 1: Table S3). GPS nodes were deployed at nine locations and in eight separate months over the course of the study (Additional file 1: Table S3). GPS nodes were scheduled to record positions every 20 min when battery voltage was between 4 and 3.8 V, every 1 h when voltage was between 3.8 and 3.4 V, and every 12 h when voltage had fallen to between 3.4 and 3.0 V. The daily solar charge was not strong enough to fully re-charge the GPS battery, and once the battery voltage dropped to a lower recording schedule it did not return to the previous, more frequent, GPS fix recording rate. Therefore, data acquisition rates were chosen to optimize the frequency and accuracy (~5 m) of recorded positions. Recorded positions were downloaded from the GPS nodes via a remote base station [41] within a range of <200 m. (These data are available in movebank.org; study name: “Movements of the Christmas Island flying fox, Australia”).

To minimize stress while fitting the GPS nodes all flying-foxes were anesthetized with vaporized isoflurane (Ohmeda Tec 4, Avon, Ohio, United States; [40] at an induction rate of 5% and maintenance rate of 1.5%, delivered in 1 L/min oxygen. Our research protocols followed the American Society of Mammalogists guidelines for research on live mammals [75], and were approved by the Animal Care and Ethics Committee of Western Sydney University (Project Protocol No. A11140). Permits to capture and process *P. natalis* were issued by the Christmas Island National Park (Permit No. CINP-2015-6-1).

Foraging movement and habitat use modeling

Movement-based kernel estimates (MBKE; [10] were created based on the GPS node data using the AdehabitatHR package (version 0.4.15; [19] in program R version 4.0.5 [70]. To identify areas with varying degrees of use,

we generated utilization distributions (UD) using the biased random bridge function [10] in the AdehabitatHR package. We generated 95% UD's to determine an individual's overall foraging range (FR). We use the term ‘foraging range’ that is defined by Bonaccorso et al. [12] as “the total area traversed by an individual as it searches for food and feeds, as well as movements between day roosts and foraging sites”. To identify and quantify the number of foraging areas (FA) that were intensively and/or repeatedly used within the FR we generated 30% intensity distributions (ID, [11]. The minimum distance between foraging areas was 15 m. We then counted the number of unique FAs visited within a night and across all nights. To further understand the potential dispersal distances provided by *P. natalis*, we calculated the distance from the roost site to all FAs visited within a night, the distance traveled between nightly used FAs, total nightly foraging dispersal distances (i.e., the distance between the furthest two GPS fixes within a night) and the long axis across the entire FR (LAX; i.e., the distance between the furthest two GPS fixes across all nights) (for a complete list of spatial measurements see Table 1). For calculations of FR, and FA we only used GPS fixes captured within the 20 min sampling interval. GPS fixes captured within the 20 and 60 min sampling intervals were used to calculate nightly dispersal distances and the number of nightly FAs visited. GPS fixes captured within the 60 min sampling interval were only used in determining the number of FAs visited when they visited a previously identified FA calculated using the 20 min sampling data. Nights with <14 GPS fixes were excluded from calculations of nightly dispersal distance and the number of nightly FAs visited. All GPS fixes across all tracking nights were used to calculate LAX (see Additional file 1: Table S3). MBKE

Table 1 Abbreviation, method of calculation, and definition or purpose for interpretation for the spatial measurements collected from 24 Christmas Island flying-foxes (*Pteropus natalis*) fitted and tracked with GPS telemetry nodes between August 2015 and November 2017

Measurement	Abbreviation	Calculation	Definition or purpose
Foraging range	FR	95% utilization distributions (UD)	The total area traversed by an individual as it searches for food and feeds, as well as movements between day roosts and foraging sites
Foraging area	FA	30% intensity distributions (ID)	Identify and quantify the number of intensively and/or repeatedly used foraging areas within the foraging range
Long axis across the foraging range	LAX	Distance between the furthest two GPS fixes across all nights	The scale of movements during the entire tracking period
Total nightly foraging dispersal distance	Nightly dispersal	Distance between the furthest two GPS fixes within a night	The scale of movements during a single night
Distance from roost to foraging areas	Roost to FA	Distance between the roost site and each nightly used foraging area	The scale of movements individuals travel from the roost site in search of food
Distance between foraging areas	Between FA	Distance between each nightly used foraging area	The scale of movements individuals travels between foraging areas in search of food

polygon data and foraging locations from GPS nodes were imported into ArcGIS v10.3.1 and overlaid onto a Christmas Island Vegetation and Clearing Map [33] at a 2 m resolution. Land-cover categories were assessed for the FR and FA of each tracked individual, identifying the number of unique vegetation habitats within each FR and FA (Additional file 1: Table S2). Over the course of this study, we were successful in tracking multiple individuals with overlapping FAs during three separate periods (Additional file 1: Table S4). For each group of simultaneously tracked individuals we calculated the area among overlapping FAs using the ‘intersect’ tool in ArcGIS (v10.3.1), and provide the percentage of overlap for each overlapping dyad. We also measured the distance between foraging locations for GPS fixes recorded with same timestamp when one or more of the simultaneously tracked individuals occupied the overlapping area of the two FAs.

Assessing foraging resource defense

An assessment of agonistic interactions between *P. natalis* individuals at foraging sites was conducted for the purpose of establishing that *P. natalis* engages in foraging resource defense. In all but one observation (see Additional file 2) the body mass and morphological measurements of all individuals observed was unknown. Therefore, we were unable to test for the effects of body size on resource defense. Interactions of foraging *P. natalis* were observed during one to three-hour long surveys ($n=272$), totaling 306 observation hours. Behaviors exhibited in the defense of foraging resources comprised: (1) ‘scent marking’, whereby an individual rubs its scapular glands along the petioles of leaves or branches; (2) ‘threat display’, whereby an individual directs loud vocalizations, wing spreading, rapid swinging of the thumb claws, at another individual; (3) ‘chase’, whereby an individual aggressively advances towards another individual in a threatening manner; and (4) ‘escalated fights’, whereby an individual uses its wings, claws, and teeth in direct physical contact with another individual (for further details refer to [49]).

The size of an individual’s defended patch was estimated by measuring the canopy of known foraging locations using aerial imagery in Google Earth Pro v7.3.3.7786 (Google, Mountain View, California, United States).

Statistical analysis

All statistical tests were two-tailed, employed an α value of 0.05, and were conducted in R version 4.05 [70]. Continuous variables are characterized by median and interquartile range (IQR). Generalized linear models (GLMs) were constructed with the ‘stats’ package to assess how

intrinsic (body mass, skeletal size, and sex) and extrinsic (rainfall, time of year, and the number of GPS fixes) variables affected differences in the size of FR, FA, LAX and the number of vegetation habitats within the FR and FA. Linear mixed-effect models (LMMs) were constructed with the ‘lme4’ package [9] to assess the distance traveled between roost sites and nightly FAs, the distance traveled between nightly used FAs, and total nightly foraging dispersal distances. A Poisson generalized mixed-effect model (GLMM) with a log-link function was constructed with the ‘lme4’ package to assess the number of nightly foraging sites visited, and a Poisson GLM with a log-link function was constructed to assess the diversity of floral resource visited. A single metric for skeletal size was estimated using the score values from a principal component analysis (PCA) on the morphological measurements of forearm length, thumb length, claw length and tibia length (see also; [85]). For all LMM and GLMM models the identity of the individual was included as a random effect to account for repeated measures. The response variables in each of the constructed GLM and LMM models sets were not normally distributed. To normalize the response variable in each of the constructed model sets, excluding the Poisson GLM, an Ordered Quantile (ORQ) normalization transformation was applied to the response variables FR, FA, LAX, distance from roost to FAs, distance between FAs, nightly dispersal distances, and foraging distance between simultaneous tracked individuals. All response variables were transformed using the ‘bestNormalize’ package [67]. The explanatory variables body mass and rainfall were rescaled using the default scale function in R. Pearson’s correlations were used to check for collinearity between explanatory variables. We chose to remove ‘the number of nights tracked’ from all models as it was highly correlated to ‘the number of positions recorded’ ($r=0.94$, $P<0.001$). For models predicting the number of pollen types found on *P. natalis*, which represents the foraging behaviors of the broader population (i.e., juveniles, sub-adults and adults of both sexes), ‘skeletal size’ was removed as it was highly correlated to ‘body mass’ ($r=0.70$, $P<0.001$). For all other models involving GPS tracked individuals there was no correlation between body mass and skeletal size ($r=0.25$, $P>0.232$) or time of year and rainfall ($r=0.06$, $P>0.795$). The full models predicting FR, FA, LAX, distance from roost to FAs, distance between FAs, nightly dispersal distances, and the number of pollen types included interactions for body mass and sex, body mass and rainfall, skeletal size and sex, and body mass and time of year (Additional file 1: Table S5). The full model for the number of pollen types included the additional variables time of capture, age class, and interactions for body mass, age class, and sex. Candidate models were

compared using Akaike Information Criterion for small sample sizes (AIC_c). We considered all models within $\Delta AIC_c \leq 2$ (Additional file 1: Table S5) to be competitive and were then averaged [3] using the ‘MuMin’ package [8]. The proportion of variance explained by the fixed effects retained in each of the models was considered by computing the R^2 values using the ‘rsq’ package for each GLM [93] and the ‘partR2’ package for each LMM and GLMM [77].

Results

Foraging ranges

The median foraging range (FR) for all 24 tracked *P. natalis* was 36.27 ha (IQR 14–329 ha) (Additional file 1: Table S6). This included an adult male with a body mass of 374 g, that was active over a much larger area (1936 ha) than any other individual. The smallest FR (4.13 ha) belonged to an adult male with a body mass of 515 g (Additional file 1: Table S6).

The median long axis across the foraging range (LAX) was 2.83 km (IQR 0.70–5.10 km) (Additional file 1: Table S6). The median nightly distance traveled from roost site to foraging area across all individuals was 216.01 m (IQR 62.73–673.18 m). The median nightly distance traveled between FAs across all individuals was 245.99 m (IQR 107.20–627.97 m). The median nightly foraging distance across all individuals and all nights was 0.54 km (IQR 0.23–0.91 km). The longest nightly foraging distance among all individuals and nights was 8.89 km by an adult male weighing 374 g, and the shortest was 3.1 m by an adult female with a body mass of 459 g.

The median foraging area (FA) was 1.07 ha (IQR 0.60–8.13 ha; Additional file 1: Table S6), which represented 3% of the median FR. Over multiple foraging nights, 54% ($n=13$) of tracked individuals foraged at 5–10 FAs, while 21% ($n=5$) foraged at <5 FAs, and 25% ($n=6$) foraged at >10 FAs (max=17, Additional file 1: Table S6), and this was not influenced by the number of GPS fixes (LMM; $R^2=28.15\%$, $Z=1.43$, $P=0.153$; supplemental material 1: Table S7). Within a single foraging night, 50% ($n=12$) of *P. natalis* foraged at multiple FAs each night and 46% ($n=11$) foraged at multiple FAs on 70–92% of all foraging nights. Only one individual foraged at a single FA on 73% of all foraging nights (Additional file 1: Table S6).

Foraging areas (FA) of individuals that were tracked simultaneously over the course of each tracking period overlapped by between 0.96 and 58.33% across all tracking nights (Additional file 1: Table S4), suggesting a shared use of foraging resources (Fig. 2a). Only two adult females tracked at Hughes Dale in October of 2017 showed no temporal or spatial overlap among their FAs (Fig. 2a; Additional file 1: Table S4). However, within a

single foraging night, FAs were, for the most part, spatially disjunct (Fig. 2b). During periods in which one of the simultaneously tracked individuals occupied the overlapping space of another individual’s FA, the median distance between foraging locations was 81.37 m (IQR: 44.75–262.01 m). There were two adult females (body mass=432 g and 466 g) who foraged within 5 m from each other in a large patch of bananas over a period of three nights (Additional file 1: Table S4); however, foraging at this area was dominated by the heavier female.

Effects of body mass on patterns of movements

Across all individuals, body mass was negatively correlated to the size of their FR (GLM; $R^2=46.19\%$, $Z=3.43$, $P<0.001$; Fig. 3a), FA (GLM; $R^2=33.31\%$, $Z=2.45$, $P<0.014$; Fig. 3b), and LAX (GLM; $R^2=33.15\%$, $Z=2.59$, $P<0.009$; Fig. 3c; Additional file 1: Table S7). Rainfall was also negatively correlated with LAX (GLM; $R^2=15.49\%$, $Z=2.01$, $P<0.044$; Additional file 1: Table S7).

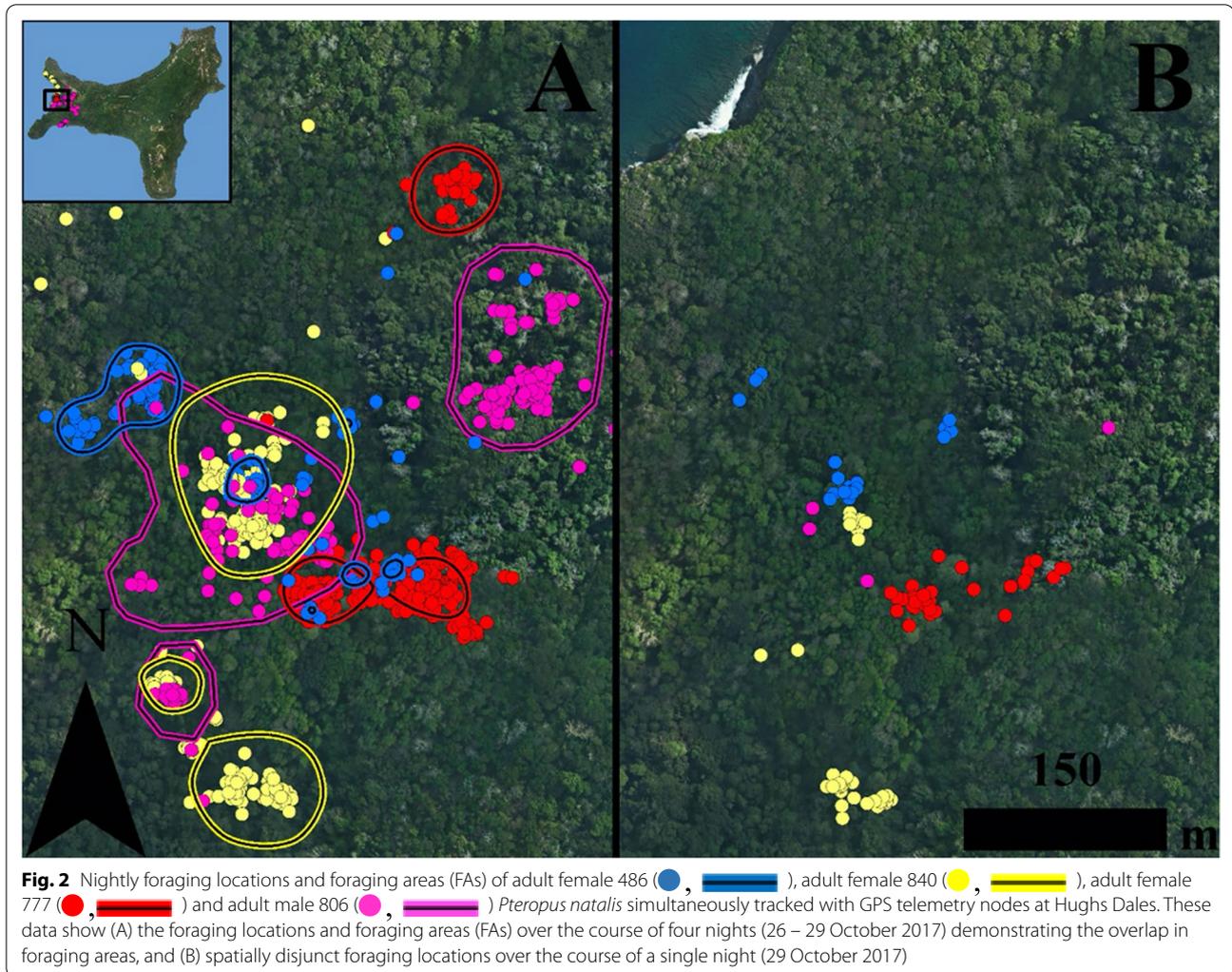
Similar to LAX, the nightly distance traveled between roost site and FAs (Fig. 4a), the distance traveled between nightly used FAs (Fig. 4b), and the nightly foraging distances (Fig. 4c), decreased significantly with increased body mass (LMM; roost to FA: $R^2=33.40\%$, $Z=2.95$, $P<0.007$; between FA: $R^2=33.99\%$, $Z=3.11$, $P<0.005$; nightly dispersal: $R^2=43.44\%$, $Z=2.57$, $P<0.010$; Additional file 1: Table S7). Additionally, the number of FAs visited by *P. natalis* over the course of a single night (Fig. 4D) was negatively correlated with body mass (GLMM; $R^2=26.93\%$, $Z=4.97$, $P<0.001$; Additional file 1: Table S7).

The number of vegetation habitats within FRs and FAs significantly increased with the size of an individual’s FR and FA (Pearson’s correlation; FR: $r=0.98$, $n=24$, $P<0.001$; FA: $r=0.77$, $n=24$, $P<0.001$) and decreased significantly with body mass for FR (GLM; $R^2=45.79\%$, $Z=3.29$, $P<0.002$) and FA (GLM; $R^2=14.68\%$, $Z=2.47$, $P<0.014$; Additional file 1: Table S7).

Sex was only retained ($\Delta AIC_c \leq 2$) in models predicting the number of pollen types (Additional file 1: Table S5) but was not found to be significant (GLMM: $R^2=2.19\%$, $Z=1.69$, $P>0.090$) after model averaging (Additional file 1: Table S7). Sex was not retained ($\Delta AIC_c \leq 2$) in any of the models constructed to explain patterns of foraging movements (Additional file 1: Table S5).

Floral diversity

The examination of pollen among all captured *P. natalis* ($n=115$) revealed that individuals had, on average, pollen from 2.94 (SD=1.92) plant species, with some individuals having pollen from as many as nine plant species. Within each of the age classes, on average, juveniles had pollen from 3.38 (SD=1.87) plant species, sub-adults



had pollen from 2.97 (SD = 1.94) plant species, and adults had pollen from 2.16 (SD = 1.77). The number of pollen types was negatively correlated with body mass in each of the juvenile, sub-adult, and adult age classes (GLM: $R^2 = 26.52\%$, $Z = 3.671$, $P < 0.001$; Fig. 5, Additional file 1: Table S7). The number of pollen types was also negatively correlated to body mass in the subset of individuals ($n = 17$) that were tracked and from which pollen counts were available (GLM: $R^2 = 46.03\%$, $Z = -2.41$, $P < 0.017$).

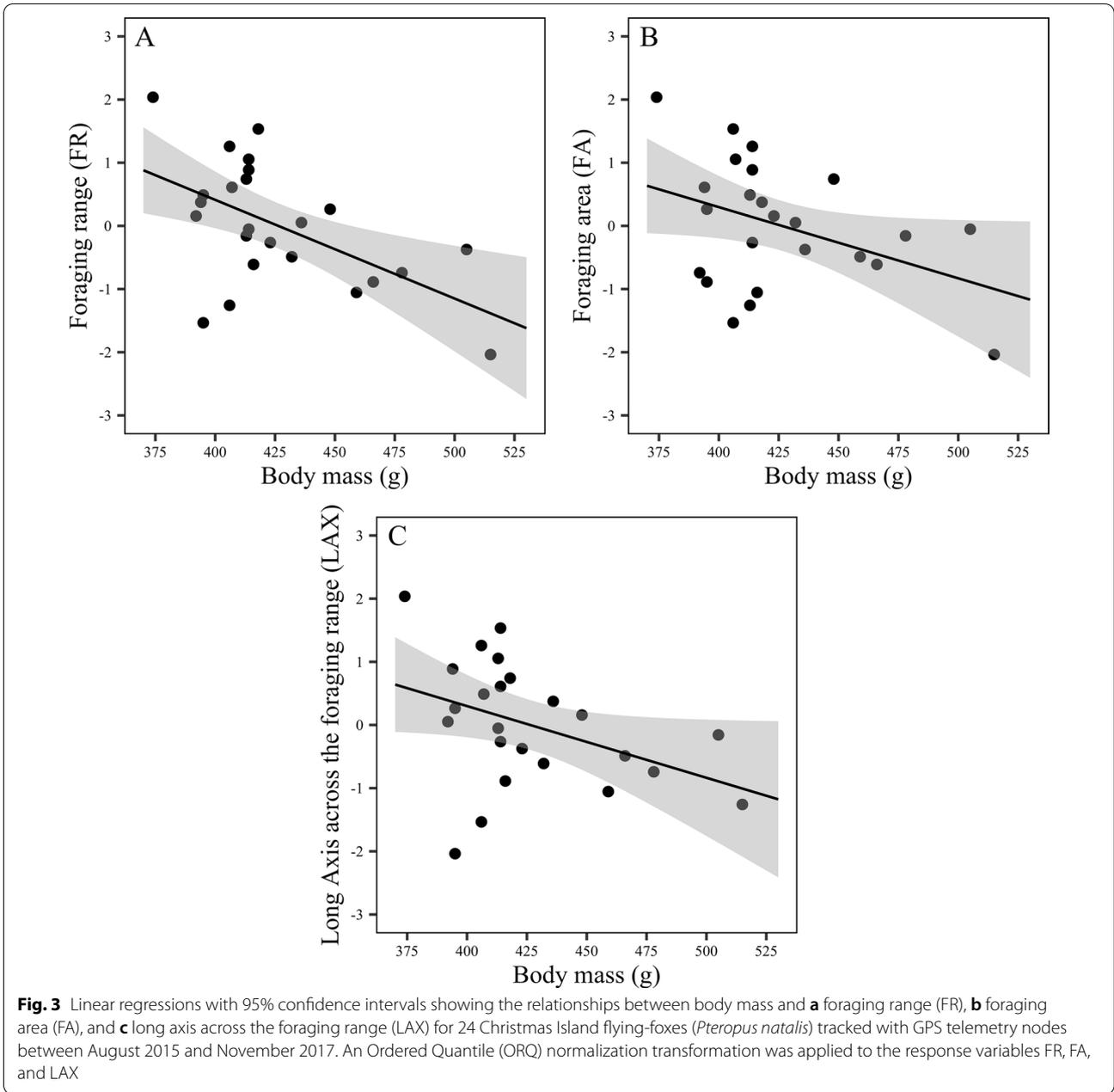
Foraging defense

Over the course of 272 surveys of flying-foxes at foraging sites, we observed 105 instances of foraging resource defense between *P. natalis* individuals. The most frequent defensive behavior observed was vocalization, followed by wing spreading, fighting and chasing. We also observed one instance of scent marking branches by a male *P. natalis* on *C. papaya* (see Additional file 2

for a detailed description of the foraging resource defense behaviors observed). Among smaller trees (e.g., *C. papaya* and *Musa* spp.), *P. natalis* for the most part defended the entire tree, although it was not unusual to see a second individual on the outskirts of the trees' branches when the canopy volume was $> 3 \text{ m}^3$. Among larger foraging trees (e.g., *Magnifera* spp. and *Ficus* spp.) multiple individuals could be seen, each defending a patch, approximately 3 m^3 , with multiple juveniles on the periphery of the tree.

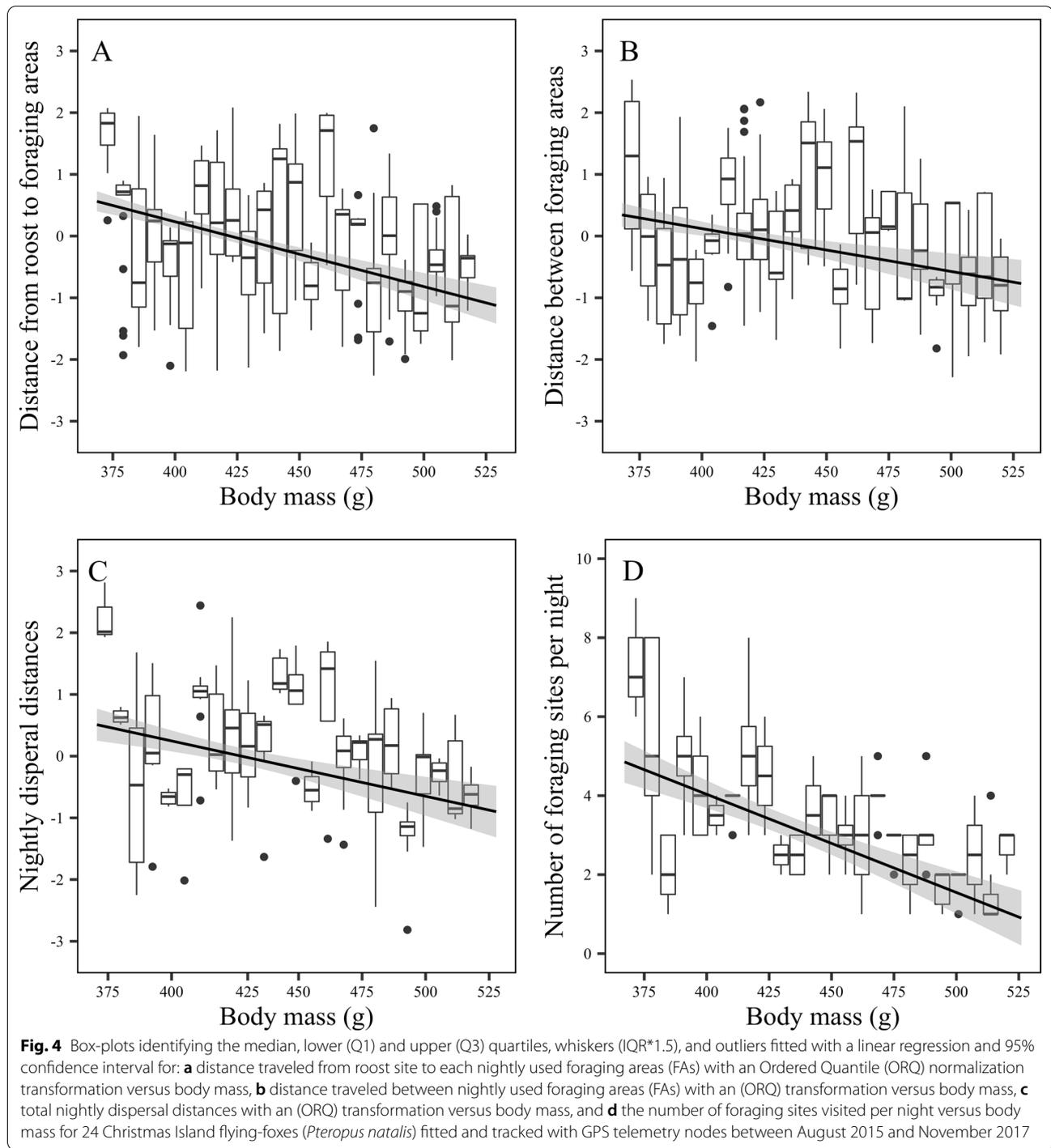
Discussion

In this study we found that morphological characteristics, primarily body mass, were linked to *P. natalis*' foraging movements. Overall, smaller individuals traveled longer distances each night, visited more foraging sites each night, and had larger foraging ranges overall, than larger conspecifics. Smaller individuals also had pollen from a higher diversity of plant taxa on their fur. Combined,



these observations suggest that, individually, smaller *P. natalis* provide longer distance pollen dispersal services to a broader range of plant species on Christmas Island than do their larger counterparts. Behavioral observations further indicated that *P. natalis* engages in foraging resource defense, and given that in territorial species, larger individuals have a clear advantage in obtaining and defending territories [76], this provides a potential mechanism for the observed body size-dependent ecosystem services of *P. natalis*.

Pteropus natalis foraging movements were negatively correlated to body mass both in terms of their magnitude and their frequency (Additional file 1: Table S7). These telemetry results are additionally supported by the results of a multi-year color band resighting program, which indicated that juveniles moved greater distances (45%) on average than adult conspecifics (C.M.T., pers., obs.). In the present study, larger *P. natalis* individuals visited fewer nightly foraging areas (Fig. 4D), traveled shorter distances from roost sites to nightly foraging areas (Fig. 4A), among nightly foraging



areas (Fig. 4B and C) and across their foraging ranges (Fig. 3D), and had smaller foraging ranges (Fig. 3A) than smaller conspecifics (Additional file 1: Table S6) who covered a greater number of vegetation habitats. The observed links between foraging movements and body size found in this study are consistent with other

studies of *Pteropus* species reporting smaller individuals traveling further distances and visiting a greater number of foraging areas than larger individuals [6, 55, 62, 63]. The dispersal of seeds and pollen plays a significant role in forest regeneration and maintenance, a key conservation issue among tropical forest ecosystems.

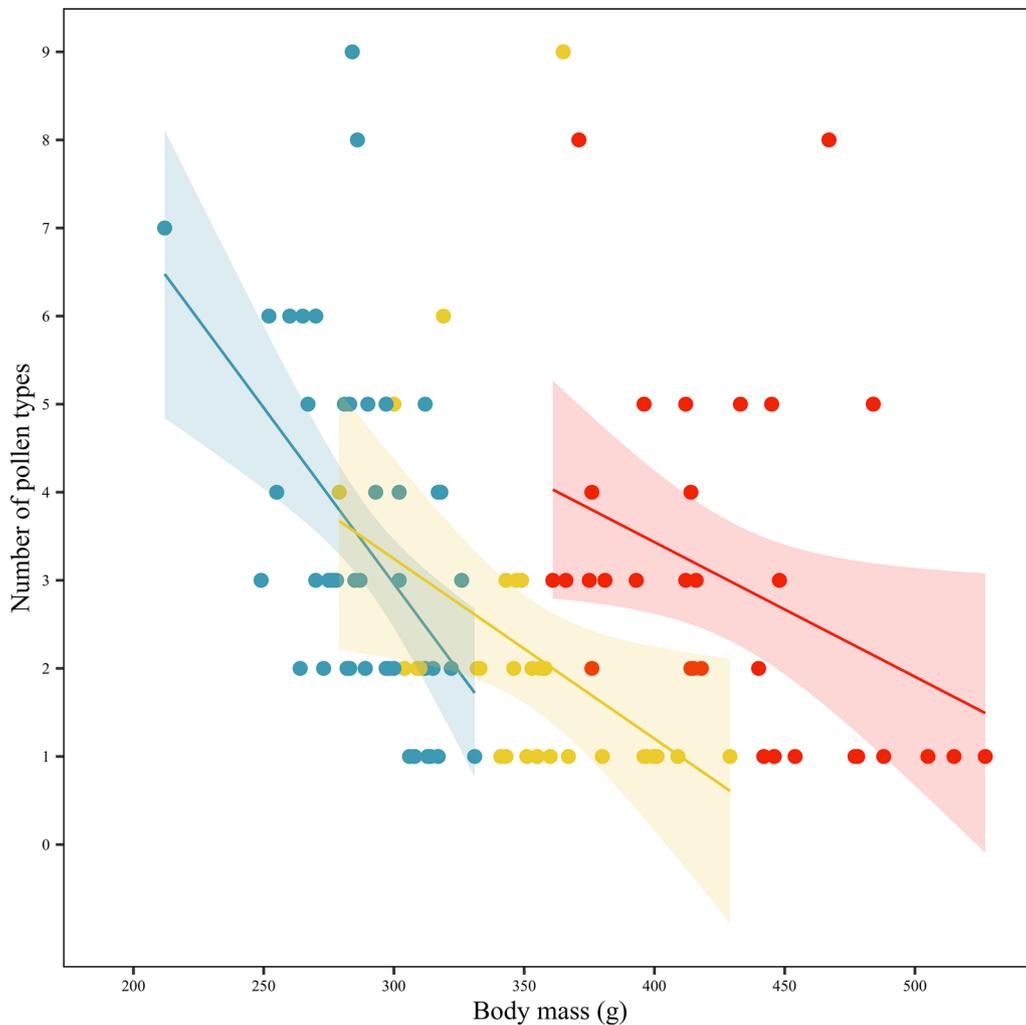


Fig. 5 Linear regression with 95% confidence intervals showing the relationship between body mass and the number of pollen types for juvenile (blue, $n = 53$), sub-adult (yellow, $n = 31$) and adult (red, $n = 31$) Christmas Island flying-foxes (*Pteropus natalis*) captured between August 2015 and November 2017

The foraging movements of *P. natalis* demonstrates their ability to serve as a plant dispersal agent. Within a night, smaller *P. natalis* visited twice as many foraging areas as larger individuals (Fig. 4D) and therefore had greater potential to disperse pollen over longer distances.

Smaller *P. natalis* foraged on a greater diversity of plant species than their larger conspecifics (Fig. 5; Additional file 1: Table S7). On average the number of pollen types found on juvenile *P. natalis* was 64% more than the number of pollen types found on adults. Since bats groom themselves extensively while roosting, it is likely that few pollen grains should be retained from one night to the next [37]; therefore, the diversity of pollen collected from an individual is most likely indicative of the plant

species visited during the night of capture. This study did not investigate the gut-passage time of seeds in *P. natalis*. However, the dispersal potential of pollen by *P. natalis* theoretically applies to the dispersal of seeds as the average gut-passage time for seeds is less than 30 min in a variety of frugivorous bat species [32, 59, 61, 78, 79, 82]. On Christmas Island the only native species, besides *P. natalis*, that serves as a disperser of both seeds and pollen is the much smaller Christmas Island white-eye (~ 14 g; *Zosterops natalis*). Although the movements of *Z. natalis* have not been studied, other *Zosterops* spp. typically have home ranges that are an order of magnitude smaller than those reported here for *P. natalis* (e.g., [1, 35], highlighting the critical nature of the long-distance pollen and

seed dispersal services that particularly smaller *P. natalis* provide on Christmas Island.

Why are foraging movements body-size dependent in *P. natalis*? For many mammals body size is positively correlated with the size of foraging and home ranges [45, 54], as larger individuals tend to have a greater intrinsic capacity for movement [18, 66, 68] and need to cover more ground to meet their daily energy requirements [45, 54]. However, in our study larger individuals were in fact less mobile than smaller individuals overall; therefore, these explanations cannot account for the observed body size-dependent foraging movement dynamics of *P. natalis*. Our behavioral observations indicated that *P. natalis* engages in foraging resource defense through a variety of agonistic behaviors, including vocalizations, wing spreading, chasing, fighting, and scent marking as similarly reported among other *Pteropus* species [6, 14, 60, 71, 81, 89, 90]. Resource defense generally functions to provide a dominant individual with an adequate supply of some critical resource (often food) at the expense of less dominant individuals (usually conspecifics; [16, 44] who are forced to move more often to acquire undefended foraging resources [16, 28]. Although not directly tested in our study, in many territorial species, dominance is linked to body size [21, 22, 38, 52, 87], and the observed body size-dependent foraging movements of *P. natalis* are consistent with those of other nectivorous animals, including bats, that actively defend foraging resources [44, 46].

It could be argued that age rather than body size explains the differences in foraging movements and pollen diversity, as body size and age are related and, in particular, volant juvenile flying-foxes may travel on long, so called 'exploratory flights' (e.g., [6]. However, while age is likely a contributing factor to differences in movements at the population level, it cannot explain the differences in movements observed in this study: tracked individuals were adults with the exception of one sub-adult. In addition, the number of pollen types found on caught individuals was negatively correlated to body mass within age class, including within the subset of tracked individuals for which pollen counts were available, clearly showing an effect of body mass on pollen diversity irrespective of age. While anecdotal observations suggest that smaller flying-fox individuals can be displaced from foraging sites by larger, dominant individuals (e.g., [53], to our knowledge, no studies of free ranging populations have directly tested whether foraging resource defense is body size-dependent in this taxon. This is likely due to the difficulty of observing individuals of known body mass interacting at foraging sites; however, diet and behavioral studies on captive populations of *P. livingstonii* demonstrated that older individuals [22], were more dominant and

defended and/or displace smaller individuals from foraging resources [52, 87].

Alternatively, *P. natalis*' size-dependent foraging movements could be the result of producer-scrounger dynamics (e.g., [7, 36]. For example, larger-sized 'scroungers' could 'eavesdrop' on the foraging success of smaller 'producers' to help them locate and then usurp foraging resources, forcing the smaller producers to move to another foraging location. However, similarly to other *Pteropus* studies [26, 50, 84], we found that tracked individuals of all sizes regularly returned to the same foraging locations night after night, implying that individuals base their foraging decisions at least in part on their prior knowledge of the locations of foraging resources. Therefore, producer-scrounger dynamics do not present a mutually-exclusive alternative to resource defense as an explanation for the body size-dependent foraging movements observed in this species. Research involving systematic behavioral observations on individuals of known body mass interacting while foraging in the wild is needed to further investigate the social dynamics of *P. natalis* and to better understand how body size-dependent social interactions affect foraging movements and their consequences for flying-fox ecosystem services.

Our findings indicate that smaller *P. natalis* are the primary contributors to long distance dispersal of pollen and seeds provided by this species. Similar results were found in populations of *P. conspicillatus*, where 'residents' appeared to provide reduced dispersal distances compared to transient 'raiders' [71]. Territorial behaviors are primarily a function of competition, which can be dependent on population densities [15, 48]. A number of studies, including those conducted on *Pteropus* species, have shown that decreasing population densities of seed dispersers and pollinators can disrupt dispersal mutualisms by reducing the quantity of propagules dispersed or the distances over which they are transported [53, 83, 92]. Reduced competitive interactions at foraging sites can affect such dispersal mutualisms in a nonlinear way, so that flying-foxes may cease to be effective plant vectors long before becoming rare [53]. Therefore, the current threatened status of *P. natalis* on Christmas Island is of concern as the effectiveness of the species as a vector of pollen and seeds may rely on the synergistic effects between competitive interactions and decreasing density, and hence population.

Conclusion

The spatial movements of *P. natalis*, which varied considerably among individuals and were significantly linked to body mass, have important implications for the reproductive biology of a large number of Christmas Island's

plant species. Animal dispersers are crucial to facilitate and maintain gene flow among many plant populations [73]. Many of Christmas Island's native plant species are "Chiropterophilous" and almost all are self-incompatible hermaphrodites that require cross-pollination to set fruit [65]. Therefore, the direct ecological impacts caused by the further decline or loss of *P. natalis* could be severe and may in turn precipitate indirect negative impacts to other species throughout Christmas Island's unique ecological communities. In addition, the maintenance of population diversity contributes to the long-term conservation of essential ecosystem processes [74], and the findings of our study imply that changes to the demographic composition of *P. natalis* could exacerbate the ecological impacts of the species' decline on Christmas Island. We therefore recommend that the disparate ecosystem services provided by the demographic diversity should be considered and incorporated more explicitly into studies and management actions of this and other insular *Pteropus* species, for a more holistic approach benefitting both flying-foxes and the ecosystems they service.

Abbreviations

MBKE: Movement-based kernel estimates; UD: Utilization distributions; FR: Foraging range; FA: Foraging area; LAX: Long axis across FR; GLM: General linear models; LMM: Linear mixed-effects model; GLMM: Generalized linear mixed-effects model; PCA: Principal component analysis; AIC: Akaike information criterion.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-022-00315-8>.

Additional file 1: Table S1. Known and suspected food plants for Christmas Island flying-foxes (*Pteropus natalis*). **Table S2.** Classification of habitat types on Christmas Island. **Figure S1.** The proportions and capture times for pollen samples collected from Christmas Island flying-foxes (*Pteropus natalis*). **Table S3.** Christmas Island flying-foxes (*Pteropus natalis*) fitted and tracked with GPS telemetry nodes. **Table S4.** Overlap in foraging metrics of simultaneously tracked Christmas Island flying-foxes (*Pteropus natalis*). **Table S5.** Akaike information criterion (AIC_c) model selection for foraging movements by the Christmas Island flying-fox (*Pteropus natalis*). **Table S6.** Foraging range movements of 24 Christmas Island flying-foxes (*Pteropus natalis*). **Figure S2.** Location data identifying movement patterns for all Christmas Island flying-foxes (*Pteropus natalis*) fit with GPS telemetry nodes between August 2015 and November 2017. **Table S7.** Results of generalized linear models predicting foraging movements of Christmas Island flying-foxes (*Pteropus natalis*).

Additional file 2. Detailed results on observations of foraging resource defense by Christmas Island flying-foxes (*Pteropus natalis*).

Acknowledgements

We thank L. Timmiss, R. Askew, Z. Wowk, A. Dorrestein, G. Custance, V. Raj, B. Hitchcock, H. Carson, N. Hamilton for their assistance in the field. We are grateful for the intellectual and logistical support provided by B. Tiernan, D. Maple, S. Flakus, J. West, S. Surridge, R. Muller, C. Pink, M. Misso and the rest of the National Park staff on Christmas Island. We are grateful to P. Johnson from the Taronga Conservation Society Australia and E. McCarthy at Western Sydney University for their help with processing pollen samples, and J. Stevenson at

The Australian National University for assistance with pollen identification. We thank two anonymous referees and associate editor Christian Voigt for their thoughtful comments on the manuscript.

Former affiliation for John M. Martin: Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney NSW, 2000, Australia. Email: John.Martin@rbgsyd.nsw.gov.au

Authors' contributions

CMT conceived the ideas with guidance from DAW, JMM, KR, JAW and AM; CMT, DAW, JMM, KR, JAW and AM designed the methodology; CMT, DAW and AM built and designed the equipment; DAW, JMM, KR, JAW supervised the research; CMT collected the data with assistance from DAW, JMM, KR, JAW, AM and JH. CMT led the analysis and writing of the manuscript. All authors contributed critically to the drafts. All authors read and approved the final manuscript.

Funding

This work was supported in part by a scholarship from the Hawkesbury Institute of the Environment at Western Sydney University, with additional funding from Taronga Conservation Society Australia, CSIRO, Royal Botanic Garden Sydney, and Christmas Island National Park.

Availability of data and materials

The GPS data supporting the conclusion of this research are available on movebank.org; study name: "Movements of the Christmas Island flying fox, Australia".

Declarations

Ethics approval and consent to participate

Our research protocols followed the American Society of Mammalogists guidelines for research on live mammals [75], and were approved by the Animal Care and Ethics Committee of Western Sydney University (Project Protocol No. A11140). Permits to capture and process *P. natalis* were issued by the Christmas Island National Park (Permit No. CINP-2015-6-1).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Author details

¹The Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW 2753, Australia. ²Commonwealth Scientific and Industrial Research Organisation (CSIRO), 47-67 Maunds St, Atherton, QLD 4883, Australia. ³Atherton, Australia. ⁴Taronga Institute of Science and Learning, Taronga Conservation Society Australia, Bradleys Head Rd, Mosman, NSW 2088, Australia. ⁵Commonwealth Scientific and Industrial Research Organisation (CSIRO), Waite Rd, Urrbrae, SA 5064, Australia.

Received: 1 December 2021 Accepted: 17 March 2022

Published online: 11 April 2022

References

1. Abe H, Ueno S, Tsumura Y, Hasegawa M. Expanded home range of pollinator birds facilitates greater pollen flow of *Camellia japonica* in a forest heavily damaged by volcanic activity. *Single-pollen genotyping*. Berlin: Springer; 2011. p. 47–62.
2. Andrews CW. On the fauna of Christmas Island. *Proc Zool Soc Lond*. 1909;1909:101–3.
3. Arnold TW. Uninformative parameters and model selection using Akaike's information criterion. *J Wildl Manag*. 2010;74:1175–8.
4. Aziz SA, McConkey KR, Tanalgo K, Sritongchuy T, Low M-R, Yong JY, Mildenstein TL, Nuevo-Diego CE, Lim V-C, Racey PA. The critical importance of Old World fruit bats for healthy ecosystems and economies. *Front Ecol Evol*. 2021;9:181.

5. Balmford A, Rosser A, Albon S. Correlates of female choice in resource-defending antelope. *Behav Ecol Sociobiol.* 1992;31:107–14.
6. Banack SA, Grant GS. Spatial and temporal movement patterns of the flying fox, *Pteropus tonganus*, in American Samoa. *J Wildl Manag.* 2002;66:1154–63.
7. Barnard CJ, Sibly RM. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim Behav.* 1981;29:543–50.
8. Barton K. MuMIn: multi-model inference. R package version. 2015;1(13):4.
9. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. arXiv preprint [arXiv:1406.5823](https://arxiv.org/abs/1406.5823) (2014).
10. Benhamou S, Cornéilis D. Incorporating movement behavior and barriers to improve kernel home range space use estimates. *J Wildl Manag.* 2010;74:1353–60.
11. Benhamou S, Riotte-Lambert L. Beyond the utilization distribution: identifying home range areas that are intensively exploited or repeatedly visited. *Ecol Model.* 2012;227:112–6.
12. Bonaccorso FJ, Todd CM, Miles AC, Gorresen PM. Foraging range movements of the endangered Hawaiian hoary bat, *Lasiurus cinereus semotus* (Chiroptera: Vespertilionidae). *J Mammal.* 2015;96:64–71.
13. Breed AC, Field HE, Smith CS, Edmonston J, Meers J. Bats without borders: long-distance movements and implications for disease risk management. *EcoHealth.* 2010;7:204–12.
14. Brooke A. More than you wanted to know about the Samoan bat, *Pteropus samoensis*. Report Department of Marine and Wildlife Resources, Pago Pago, American Samoa; 1998.
15. Brown JL. The evolution of diversity in avian territorial systems. *Wilson Bull.* 1964;76:160–9.
16. Brown JL, Orians GH. Spacing patterns in mobile animals. *Annu Rev Ecol Syst.* 1970;1:239–62.
17. Burt WH. Territoriality and home range concepts as applied to mammals. *J Mammal.* 1943;24:346–52.
18. Burton OJ, Phillips BL, Travis JM. Trade-offs and the evolution of life-histories during range expansion. *Ecol Lett.* 2010;13:1210–20.
19. Calenge C. Home range estimation in R: the adehabitatHR package. R package 0.4.15; 2011.
20. Clutton-Brock T, Green D, Hiraiwa-Hasegawa M, Albon S. Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behav Ecol Sociobiol.* 1988;23:281–96.
21. Clutton-Brock TH. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press; 1988.
22. Courts S. General behaviour and social interactions in a group of Livingstone's fruit bats *Pteropus livingstonii* at Jersey Wildlife Preservation Trust. Dodo-J Wildl Preserv Trusts. 1997;33:154–154.
23. Courts S. Dietary strategies of Old World fruit bats (Megachiroptera, Pteropodidae): how do they obtain sufficient protein? *Mammal Rev.* 1998;28:185–94.
24. Cox PA, Elmqvist T, Pierson ED, Rainey WE. Flying foxes as strong interactors in South Pacific island ecosystems: a conservation hypothesis. *Conserv Biol.* 1991;5:448–54.
25. Cox PA, Elmqvist T, Pierson ED, Rainey WE. Flying foxes as pollinators and seed dispersers in Pacific island ecosystems. In: Pacific Flying Foxes: Proceedings of and International Conference. U.S. Department of the Interior Fish and Wildlife Service Washington DC 20240, 18–23; 1992.
26. De Jong C, Field H, Tagtag A, Hughes T, Dechmann D, Jayme S, Epstein J, Smith C, Santos I, Catbagan D. Foraging behaviour and landscape utilisation by the endangered golden-crowned flying fox (*Acerodon jubatus*), the Philippines. *PLoS ONE.* 2013;8:e79665.
27. Department of the Environment. Commonwealth Conservation Advice for *Pteropus natalis* (Christmas Island flying-fox) pp. 15. Parks Australia, Canberra, Australia; 2014.
28. Dill LM. An energy-based model of optimal feeding-territory size. *Theor Popul Biol.* 1978;14:396–429.
29. Doherty TS, Fist CN, Driscoll DA. Animal movement varies with resource availability, landscape configuration and body size: a conceptual model and empirical example. *Landsc Ecol.* 2019;34:603–14.
30. Elmqvist T, Cox PA, Rainey WE, Pierson ED. Restricted pollination on oceanic islands: pollination of *Ceiba pentandra* by flying foxes in Samoa. *Biotropica.* 1992;24:15–23.
31. Epstein JH, Olival KJ, Pulliam JR, Smith C, Westrum J, Hughes T, Dobson AP, Zubaid A, Rahman SA, Basir MM. *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *J Appl Ecol.* 2009;46:991–1002.
32. Fleming TH, Heithaus ER. Frugivorous bats, seed shadows, and the structure of tropical forests. *Biotropica.* 1981;13:45–53.
33. Geoscience A. Christmas Island Vegetation and Clearing Map. Geoscience Australia. Retrieved from <https://data.gov.au/dataset/ds-ga-068a83fa-5736-7037-e054-00144fdd4fa6/details?q=Christmas%20Island> (2014).
34. Gibson CA. A note on the mammals of Christmas Island. *Bull Raffles Mus Singap.* 1947;18:166–7.
35. Habel JC, Hillen J, Schmitt T, Fischer C. Restricted movements and high site fidelity in three East African cloud-forest birds. *J Trop Ecol.* 2016;32:83–7.
36. Harten L, Matalon Y, Galli N, Navon H, Dor R, Yovel Y. Persistent producer-scrounger relationships in bats. *Sci Adv.* 2018;4:e1603293.
37. Heithaus ER, Fleming TH, Opler PA. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. *Ecology.* 1975;56:841–54.
38. Jackson WM. Can individual differences in history of dominance explain the development of linear dominance hierarchies? *Ethology.* 1988;79:71–7.
39. James DJ, Dale GJ, Retallick K, Orchard K. Christmas Island flying-fox *Pteropus natalis* Thomas 1887: an assessment of conservation status and threats. Christmas Island National Park, Commonwealth of Australia; 2007. p. 55.
40. Jonsson N, Johnston S. Field anaesthesia of three Australian species of flying fox. *Vet Rec.* 2004;154:664–664.
41. Jurdak R, Sommer P, Kusy B, Kottege N, Crossman C, Mckeown A, Westcott D. Camazotz: multimodal activity-based GPS sampling. In: Proceedings of the 12th international conference on information processing in sensor networks. ACM; 2013. p. 67–78.
42. Karubian J, Durães R. Effects of seed disperser social behavior on patterns of seed movement and deposition. *Oecol Bras.* 2009;13:45–57.
43. Khamcha D, Savini T, Westcott DA, McKeown A, Brockelman WY, Chimchome V, Gale GA. Behavioral and social structure effects on seed dispersal curves of a forest-interior Bulbul (Pycnonotidae) in a tropical evergreen forest. *Biotropica.* 2014;46:294–301.
44. Lemke TO. Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. *Ecology.* 1984;65:538–48.
45. Lindstedt SL, Miller BJ, Buskirk SW. Home range, time, and body size in mammals. *Ecology.* 1986;67:413–8.
46. Linhart YB. Ecological and behavioral determinants of pollen dispersal in hummingbird-pollinated Heliconia. *Am Nat.* 1973;107:511–23.
47. Lumsden L. The extinction of the Christmas Island pipistrelle. *Australas Bat Soc NewsL.* 2009;33:22–7.
48. MacArthur RH. The theory of the niche. In: Population biology and evolution; 1968. p. 159–76.
49. Markus N, Blackshaw JK. Behaviour of the black flying fox *Pteropus alecto*: 1. An ethogram of behaviour, and preliminary characterisation of mother-infant interactions. *Acta Chiropterol.* 2002;4:137–52.
50. Markus N, Hall L. Foraging behaviour of the black flying-fox (*Pteropus alecto*) in the urban landscape of Brisbane, Queensland. *Wildl Res.* 2004;31:345–55.
51. Marshall AG. Old World phytophagous bats (Megachiroptera) and their food plants: a survey. *Zool J Linn Soc.* 1985;83:169–351.
52. Masefield W. Forage preferences and enrichment in a group of captive Livingstone's fruit bats *Pteropus livingstonii*. Dodo-J Wildl Preserv Trusts. 1999;35:48–56.
53. McConkey KR, Drake DR. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology.* 2006;87:271–6.
54. McNab BK. Bioenergetics and the determination of home range size. *Am Nat.* 1963;97:133–40.
55. McWilliam A. The feeding ecology of *Pteropus* in north-eastern New South Wales, Australia. *Myotis.* 1986;23:201–8.
56. Mickleburgh SP, Hutson AM, Racey PA. Old World fruit bats: an action plan for their conservation. Gland: IUCN; 1992.
57. Mildenstein TL, Stier SC, Nuevo-Diego CE, Mills LS. Habitat selection of endangered and endemic large flying-foxes in Subic Bay, Philippines. *Biol Conserv.* 2005;126:93–102.
58. Mokany K, Prasad S, Westcott DA. Impacts of climate change and management responses in tropical forests depend on complex frugivore-mediated seed dispersal. *Glob Ecol Biogeogr.* 2015;24:685–94.

59. Nakamoto A, Kinjo K, Izawa M. The role of Orii's flying-fox (*Pteropus dasy-mallus inopinatus*) as a pollinator and a seed disperser on Okinawa-jima Island, the Ryukyu Archipelago, Japan. *Ecol Res.* 2009;24:405–14.
60. Nelson JE. Behaviour of Australian pteropodidae (Megacheroptera). *Anim Behav.* 1965;13:544–57.
61. Oleksy R, Giuggioli L, McKetterick TJ, Racey PA, Jones G. Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. *PLoS ONE.* 2017;12:e0184023.
62. Oleksy R, Racey PA, Jones G. High-resolution GPS tracking reveals habitat selection and the potential for long-distance seed dispersal by Madagascan flying foxes *Pteropus rufus*. *Glob Ecol Conserv.* 2015;3:678–92.
63. Palmer C, Woinarski J. Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the Northern Territory: resource tracking in a landscape mosaic. *Wildl Res.* 1999;26:823–38.
64. Parks DON. Status of the Christmas Island flying fox: Results from the 2016 island-wide monitoring program. Parks Australia, Canberra, Australia; 2016. p. 27.
65. Payens J. A monograph of the genus *Barringtonia*. *Blumea.* 1967;15:157–263.
66. Perry G, Garland T Jr. Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology.* 2002;83:1870–85.
67. Peterson RA, Peterson MRA. Package 'bestNormalize'. Normalizing transformation functions. R package version, 1; 2020.
68. Phillips BL, Brown GP, Webb JK, Shine R. Invasion and the evolution of speed in toads. *Nature.* 2006;439:803–803.
69. Pijl LVD. The dispersal of plants by bats (chiropterochory). *Acta Bot Neerl.* 1957;6:291–315.
70. R Core Team. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org/ (2017).
71. Richards G. The spectacled flying fox, *Pteropus conspicillatus* (Chiroptera: Pteropodidae), in north Queensland. 2. Diet, seed dispersal and feeding ecology. *Aust Mammal.* 1990;13:25–31.
72. Roithmair ME. Male territoriality and female mate selection in the dart-poison frog *Epipedobates trivittatus* (Dendrobatidae, Anura). *Copeia.* 1994;1994:107–15.
73. Russo SE, Portnoy S, Augspurger CK. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology.* 2006;87:3160–74.
74. Schindler DE, Hilborn R, Chasco B, Boatright CP, Quinn TP, Rogers LA, Webster MS. Population diversity and the portfolio effect in an exploited species. *Nature.* 2010;465:609.
75. Sikes RS. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J Mammal.* 2016;97:663–88.
76. Sokolovska N, Rowe L, Johansson F. Fitness and body size in mature odonates. *Ecol Entomol.* 2000;25:239–48.
77. Stoffel MA, Nakagawa S, Schielzeth H. parR2: partitioning R2 in generalized linear mixed models. *PeerJ.* 2021;9:e11414.
78. Tang Z-H, Mukherjee A, Sheng L-X, Cao M, Liang B, Corlett RT, Zhang S-Y. Effect of ingestion by two frugivorous bat species on the seed germination of *Ficus racemosa* and *F. hispida* (Moraceae). *J Trop Ecol.* 2007;23:125–7.
79. Tedman R, Hall L. The morphology of the gastrointestinal tract and food transit time in the fruit bats *Pteropus alecto* and *P. poliocephalus* (Megachiroptera). *Aust J Zool.* 1985;33:625–40.
80. Tidemann CR. A study of the status, habitat requirements and management of the two species of bat on Christmas Island (Indian Ocean). Final report. Zoology Department, Australian National University, Canberra, Australia; 1985.
81. Trehwella WJ, Rodriguez-Clark KM, Davies JG, Reason PF, Wray S. Sympatric fruit bat species (Chiroptera: Pteropodidae) in the Comoro Islands (Western Indian Ocean): diurnality, feeding interactions and their conservation implications. *Acta Chiropterol.* 2001;3:135–47.
82. Utzurrum R. Differential ingestion of viable vs nonviable *Ficus* seeds by fruit bats. *Biotropica.* 1991;23:311–2.
83. Wang BC, Sork VL, Leong MT, Smith TB. Hunting of mammals reduces seed removal and dispersal of the afro-tropical tree *Antrocaryon klaine-anum* (Anacardiaceae). *Biotropica.* 2007;39:340–7.
84. Weber N, Duengkae P, Fahr J, Dechmann DK, Phengsakul P, Khumbucha W, Siriaroonrat B, Wacharapluesadee S, Maneeorn P, Wikelski M. High-resolution GPS tracking of Lyle's flying fox between temples and orchards in central Thailand. *J Wildl Manag.* 2015;79:957–68.
85. Welbergen JA. Timing of the evening emergence from day roosts of the grey-headed flying fox, *Pteropus poliocephalus*: the effects of predation risk, foraging needs, and social context. *Behav Ecol Sociobiol.* 2006;60:311–22.
86. Welbergen JA, Meade J, Field HE, Edson D, McMichael L, Shoo LP, Praszczalek J, Smith C, Martin JM. Extreme mobility of the world's largest flying mammals creates key challenges for management and conservation. *BMC Biol.* 2020;18:1–13.
87. Welch MJ, Smith T, Hosie C, Wormell D, Price E, Stanley CR. Social experience of captive livingstone's fruit bats (*Pteropus livingstonii*). *Animals.* 2020;10:1321.
88. Westcott DA, Benrupperbäumer J, Bradford MG, McKeown A. Incorporating patterns of disperser behaviour into models of seed dispersal and its effects on estimated dispersal curves. *Oecologia.* 2005;146:57–67.
89. Wiles GJ, Engbring J, Falanruw MV. Population status and natural history of *Pteropus mariannus* on Ulithi Atoll, Caroline Islands. *Pac Sci.* 1991;45:76–84.
90. Wiles GJ, Johnson NC. Population size and natural history of Mariana fruit bats (Chiroptera: Pteropodidae) on Sarigan, Mariana Islands. *Pac Sci.* 2004;58:585–96.
91. Woinarski JC, Burbidge AA, Harrison PL. The action plan for Australian mammals 2012. Collingswood Victoria: CSIRO Publishing; 2014.
92. Wright SJ, Zeballos H, Dominguez I, Gallardo MM, Moreno MC, Ibáñez R. Poachers alter mammal abundance, seed dispersal, and seed predation in a Neotropical forest. *Conserv Biol.* 2000;14:227–39.
93. Zhang D. rsq: R-squared and related measures. R package version, 1; 2018.
94. Zwolak R. How intraspecific variation in seed-dispersing animals matters for plants. *Biol Rev.* 2018;93:897–913.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

