RESEARCH





Flight behaviour and short-distance homing by nomadic grey-headed flying-foxes: a pilot study

Jessica Meade^{1*}, John M. Martin^{1,2}, Adam McKeown³, Christopher Turbill^{1,4}, Melissa J. Walker^{1,5}, Wayne S. J. Boardman⁶ and Justin A. Welbergen¹

Abstract

Background The ability to navigate is crucial to the survival of many flying animals. Though relatively much less is known about the navigational abilities of bats versus birds, recent progress has been made in understanding the navigational abilities of cave roosting bats, but little is known about those of arboreal roosting flying-foxes, despite their extreme mobility.

Methods We use extremely high spatiotemporal resolution GPS tracking to examine the flight behaviour of 11 grey-headed flying-foxes (*Pteropus poliocephalus*) displaced 16.8 km from their roost. We examined flight metrics of the resulting high-resolution traces to understand whether the displaced animals were aware their location with respect to the roost of capture. We use 7 grey-headed flying-foxes tracked from the roost of capture—as part of a separate, concurrent study—to aid in this comparison.

Results Ten of 11 displaced individuals were detected at the roost of capture within four days of release, but all displaced individuals roosted for at least one night away from the roost of capture. Six individuals returned 'home' the next day, and four roosted away from 'home' for ≥ one further night. Prior to their return 'home', displaced individuals on average flew 2.7 times further and stopped 1.7 more times than reference individuals or displaced animals that had already returned 'home'. This indicates that displaced individuals expended more effort each night than non-displaced individuals. This suggests that these individuals were attempting to return 'home', rather than choosing not to return due to a lack of motivation to home. Flight segments of displaced individuals were higher, less straight, and less likely to be oriented. Flight segments that ended in a point that an individual had previously visited were faster, higher, and straighter than those not known to end in a point previously visited.

Conclusions Our findings suggest that approximately half of the displaced animals were aware of where they were with respect to 'home' the night after release, whereas other individuals took at least a further night to orient themselves. While our results are consistent with previous work suggesting that non-echolocating bats may use a large-scale navigational map based on vision, sensory manipulations would be needed to confirm this.

Keywords Bats, Fruit bat, Navigation, Pteropus

*Correspondence: Jessica Meade J.Meade@westernsydney.edu.au Full list of author information is available at the end of the article



© The Author(s) 2025. **Open Access** This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, 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 you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. 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-nc-nd/4.0/.

Background

Navigation is a critical component of animal survival, and aerial animals in particular are likely to have been under strong selection pressure for navigation ability [1]. Bats (with birds) are one of only two volant vertebrate groups, with many species exhibiting long distance flights during foraging [2-4], seasonal migration [5-7], and nomadic movements [8, 9]. The navigational ability of bats is relatively less well studied, due mainly to methodological constraints [10, 11], and remains one of the most poorly understood topics in animal behaviour [10, 12]. Despite this, in recent decades it has been shown that insectivorous microbats can use the geomagnetic field as a compass cue [13-16] and that some bats calibrate their magnetic compass using sunset cues [14, 17]. Bats are also able to detect stars [18], but celestial cues have not been shown to be used as a compass cue. Recent studies of the cave roosting Egyptian fruit bat (Rousettus aegyptiacus) demonstrated that these bats develop large scale navigational maps based on vision [4, 19], although it is unlikely that this type of navigational map could extend far beyond the areas visited by animals. It has been suggested that bats may use the geomagnetic field as a largescale navigational map extending beyond areas visited [10], but as yet this has not been confirmed experimentally [13]. Thus, while advances in tracking technology have enabled progress in the field of bat navigation, more research is required [12, 20], and particularly on arboreal roosting bats that have access to a different set of navigational cues than cave roosting species.

Flying-foxes of the Pteropus genus are amongst the most mobile bat species in the world [8], and are likely to have evolved sophisticated spatial mapping systems because they occupy complex habitats [21], and because their foraging resources (pollen, nectar and fruit) are predictable, at least in the short term [22]. Animals with predictable food resources are selected to devote brain space to spatial tracking systems [22], shown to be associated with a larger olfactory bulb size [23], which is thought to have a navigational function [22]. Species of *Pteropus* play extremely important roles in terms of pollination and seed dispersal [24], yet are increasingly threatened, with 38 of the extant species of Pteropus in the IUCN threatened categories. The grey-headed flying-fox (Pteropus poliocephalus) is classified as 'vulnerable' under federal legislation [25] and by the IUCN [26]. Threats include habitat loss, extreme heat, and biological urbanisation [26]. In some cases, management of human-wildlife conflict caused by urbanisation has led to colony dispersals [27]. Despite a number of tracking studies on arboreal roosting flying-foxes [8, 9, 28-37], how flying-foxes navigate has never been investigated, and moreover, the sensory (magnetic, visual, olfactory) basis of flying-fox navigation remains unknown. Arboreal roosting flying-foxes have high mobility among roosts [8, 38], and many roosts are available to them, which further hampers navigational research due to the lack of a known goal location. The lack of knowledge on how this highly volant group of animals navigate is thus a key knowledge gap for animal navigation studies [10].

In the present study our aim was to record high resolution homing paths of grey-headed flying-foxes as they navigated back to the roost of capture following a shortdistance displacement. We chose to conduct the experiment at a roost site in Adelaide, South Australia. This roost was chosen because it is located at the extreme westerly extent of the species' range, and at the time of our experiments there were no other roosts within 500 km. This therefore provided a useful opportunity for conducting homing experiments in Pteropus spp., as it could reasonably be assumed that individuals would attempt to navigate back to the roost where they had been caught. We released 11 grey-headed flying-foxes from a site located 16.8 km from the roost of capture, and we predicted that they would return directly to the same roost. We examine their high resolution flight paths in terms of orientation [39] and other flight metrics. In addition, we opportunistically compare the movements of the displaced animals with 'reference' individuals (n=7) that had been released and tracked from the roost for a concurrent separate study. We examined whether flight segments were oriented towards a goal [39], with the prediction that flight segments ending at a known goal were more likely to be oriented, and that non-displaced animals were more likely to perform oriented flights. We also performed exploratory analyses to determine whether any other aspect of flight patterns could be used to determine whether an individual was aware of where it was with respect to a known goal. We discuss the results in terms of flight patterns, potential navigation systems used, and future experimental design.

Methods

Species and Research Site

Grey-headed flying-foxes are among the largest *Pteropus* species weighing 600–1,100 g [40]. They are sexually dimorphic, and the mating system involves a single male and an unstable group of \geq five females [41]. Maximum sexual activity occurs from mid-March to early April, and during this time males are observed to return early to the colony before dawn immergence [42]. Females give birth in October and young are weaned between February and April [43, 44].

Grey-headed flying-foxes were caught at the Botanic Park roost located in the city of Adelaide (location: 34.92° S, 138.61° E; altitude: 49 m above sea level) between 23rd-26th July 2018 (Supplementary Table 1). At this time, female flying-foxes are likely to be in early pregnancy, and will no longer have dependant pups. Flyingfoxes were captured using mist nets during the dawn fly-in and were kept in an individual cloth bag until processing. Each flying-fox was sexed and forearm and body mass measurements were taken. Body condition was estimated on a scale of 1-5 (1 being significantly below, and 5 being significantly above, expected body condition), age was estimated based on molar wear [following; 42, 45]. We used only flying-foxes with a mass of more than 600 g (mean mass ± SD, 771.9 ± 99.6 g, range 626—973 g) to ensure that the mass of the trackers (24 g) represented less than 5% of the body mass of the tracked individuals. Flying-foxes were anaesthetised using the inhalation agent isoflurane [46] and fitted with telemetry devices (see below). After processing, flying-foxes were kept singly in pet carry cages (c. $1 \text{ m} \times 40 \text{ cm} \times 40 \text{ cm}$) until their release. Procedures were approved by the Western Sydney University Animal Care and Ethics Committee (A12217) and SA Scientific License (M26735).

Telemetry devices and attachment

Adult grey-headed flying-foxes were equipped with a lightweight GPS tracking device [Camazotz; 47]. The devices were enabled to download data wirelessly when within 500 m of a base station (located at the roost). When the devices were within radio range of another GPS tracking device, the identity of the tracker and the time it was detected was recorded [47]. The dimensions of the GPS tracker were 52 mm (length)×23 mm (width) \times 12 mm (height), with an overall mass of 24.0 g. The logger was glued to the back of anaesthetised flyingfoxes following the methods in [48] and for the purposes of this study was potted in electrical heat shrink tubing. In short, a 2.3 cm×5.2 cm patch of fur, directly above the animal's centre of gravity, was trimmed to 2-3 mm length, and skin adhesive (Sauer-Hautkleber ${}^{^{\rm TM}}\!\!)$ was applied to the patch of fur and allowed to dry for 5 min. The back of the logger was coated with 100% ethyl isocyanoacrylate glue and pressed onto the bed of tissue glue. The logger was then held in place for 10–15 min, until the ethyl isocyanoacrylate glue had dried [48]. GPS trackers for the displaced animals (n=11) were programmed to log data at 1 s intervals, whereas the remaining trackers (n = 7; designed to last for a greater number of days) wereprogrammed to record positional data at 1 s intervals, but to stop collecting data when animals were stationary (see below for study design).

Study design

18 grey-headed flying-foxes were captured and fitted with GPS trackers as part of two separate studies. 11 animals

were subjected to a short distance displacement (see 'release' below). As part of a separate study, conducted contemporaneously, seven grey-headed flying-foxes were captured and in addition to the fitting of GPS trackers, were surgically implanted with Temperature-sensitive VHF FM radio transmitters (model PD-2TH, 3.4 g; Holohil, Ontario, Canada). These transmitted core body temperature only when within range of the recorders located at the roost [49, 50], and therefore body temperature of these animals is not considered in this study [but see; 49, 50]. Males were targeted for the temperature study because for ethical reasons we did not want to operate on female flying-foxes that are likely to be in early pregnancy in July [41]. Due to a limited number of animals caught during the field work, this meant that majority of displaced animals (10/11) were female. For analytical purposes (see 'Flight metrics (all animals)' below) we divided the movement paths of the displaced animals into flights before and after the animals had returned to the roost of capture. We refer to these as 'homing' flights, and 'nonhoming' flights, respectively. Flights after the displaced animals have reached the roost of capture are considered 'non-homing' as we know that the animal has reached a place that it has been before. Fewer 'non-homing' than 'homing' flights were recorded for displaced animals as the GPS trackers tended to run out of batteries within c. 2 days. We therefore used the flight paths of the male animals released at the roost of capture as additional 'non-homing' flights and refer to these animals as 'reference' animals. Despite the sex ratio imbalance between the 'homing' and 'non-homing' flights, the study was performed at a time when body condition is likely to be increasing for both sexes, and neither sex are subject to an increase in energy expenditure (e.g. neither lactation for females or the breeding season for males) [42], thus no significant variation in foraging strategy would be expected. In addition, previous work on a different flying-fox species suggests that body mass rather than sex impacts foraging movements [51], and in the current study the mean weight of the males and females only differed by 20 g (males: mean=784 g±114 SD; female: 762 $g \pm 92$; Supplementary Table 1), thus despite the sex imbalance, the comparison between the 'homing' and 'non-homing' flights provides a useful addition to this study.

Release

Displaced individuals were released at the same location 16.8 km from the roost (34.83° S, 138.76° E; altitude, 361 m above sea level). Flying-foxes are known to make nightly foraging trips of up to 80 km [29, 52], though the mean foraging distance from a colony is \leq 13 km [38]. The high-resolution GPS loggers that we had available

[Camazotz; 47] involved download to a base station, and had a limited battery life of c. two days at a sampling rate of 1 Hz. We therefore chose a release site that balanced a navigation challenge with the need for animals to successfully return to the colony within c. 2 days in order to obtain data. We chose an accessible release site 16.8 km from the roost of capture located in an area that animals previously tracked from the Adelaide roost [37] had not visited. Before release, all animals were given fruit juice as this has previously been shown to facilitate an animal's direct return to their roost [4]. In addition, all animals were released relatively late in the night, and we therefore predicted that all animals would return directly to the roost of capture. Animals were released from 04:00 to 05:15 on the morning after capture (24th-27th July), 3.25-2.00 h before sunrise. A maximum of 6 individuals were released on a single night (see Supplementary Table 1). To mitigate the unlikely possibility that individuals would navigate back to the roost as a group, flying-foxes were released at intervals of at least 15 min. Translocation was done by car, driving the flying-foxes a total ground distance of 21 km to get to the release site. During transport, flying-foxes were held inside pet carry cages, and the inside of the car was kept at ambient temperature. The reference animals (n=7 males) were released at the roost during daylight hours the day after capture, where they reintegrated into the roost before the dusk emergence. They were transported to the roost on foot from Adelaide Zoo inside pet carry cages.

Data Handling and Analysis

Tracking data were pre-processed following the pipeline described in Gupte et al. [53]. Unreliable positions were removed using speed as a filter: positions associated with ground speeds>than the 99th percentile for each individual were removed. These values ranged from 12.6–17.4 m/s, which is greater than the estimated flight speed of grey-headed flying-foxes (8.6 m/s [54], 11.2 m/s [55]) and approaches the maximum recorded ground speed for grey-headed flying-foxes (17.5 m/s [9]), so it is unlikely that any true positions were filtered out. Next, small-scale location errors were reduced by applying a median smoothing with a moving window (K) of 5 s [53]. Finally, residence time within a 50 m radius was calculated [53], and this was used to identify areas where the animals stopped flying for more than 10 min [following 4]. We used the locations of these 'stops' to divide all nightly flights into flight segments and used these flight segments as units for analysis (see below). For each of the 11 displaced animals we determined 'homing time' based on the time of release and the time that a GPS location occurred within 500 m of the roost location. For animals for which a full movement path from the release site to the roost was not available, we searched each tracker's 'radio contact log' to identify the first time at which any tracker was detected at the roost (see Supplementary Table 1). All pre-processing and analysis was done using the R software program [56] interfaced with RStudio [57].

Orientation

We were interested in examining whether individuals were oriented towards their goal, i.e. whether flight paths are more suitably represented as correlated random walks (CRW; random search path) or as biased correlated random walks (BCRW; oriented path) [39]. This is complicated when goal locations vary between individuals, when flight paths are short, and when individuals change movement strategies within a movement path [39], i.e. shift between random search vs. oriented movement. We therefore used the procedure described in [58] to identify the point in a flight path that an animal became oriented towards a goal. This procedure involves starting from the end point of a segment (at the 'goal' location) and moving backwards along the path, measuring the backward beeline for any given point (the straight-line distance between the 'goal' and the given point). If the animal is actively orienting towards the 'goal' location, then the backwards beeline distance should be proportional to the backward pathlength distance (i.e. the distance actually travelled); whereas, if the animal reached the goal location by chance, the backwards beeline distance should be proportional to the square root of the backwards pathlength [39, see also Figs. 2 & 3 in 58]. Each flight segment was standardized to a step length of 100 m [59] using the R function TrajRedescretize [60]. The backwards beeline was plotted against the backwards path length, and the point in the movement path that the individual became oriented towards the 'goal' was identified by selecting the point at which the coefficient of determination (R^2) between the backwards path length and backwards beeline distance dipped and remained below 0.99. In other studies, this point has been selected by eye, but we aimed to reduce any potential bias and an R^2 of 0.99 captured straight paths as oriented but also allowed small deviations from a straight line (see Supplementary Fig. 1). The proportion of each flight segment that was oriented was calculated, and the absolute length of the oriented portion was calculated. Any flight segments shorter than 1 km or that did not have a known start or end location (e.g., due to data points missed due to a lack of GPS signal) were not analysed.

Flight metrics (all animals)

For every individual, for each night that complete data were available, we calculated the distance travelled, and the number of stops that lasted longer than 10 min. Nights were classified as 'homing' if individuals had been displaced from the roost and had not yet returned. Nights were classified as 'non-homing' if the individual had either been released at the roost (reference animals) or had roosted at the roost of capture the previous day (displaced animals). To examine whether there was a difference in the distance travelled, or the number of stops (longer than 10 min) we used mixed effects models with 'homing' and 'non-homing' nights as an explanatory variable, and animal identity as a random effect. Distance travelled was modelled with a linear mixed effects model, and number of stops with a generalised linear mixed effects model (Poisson family).

Next, for each flight segment for each individual, we calculated the mean ground speed, the mean height above ground, the straightness index, the percentage of the flight segment that was oriented, and the length of the flight segment. We then compared these metrics for 'homing' and 'non-homing' flight segments using mixed effects models with animal identity as a random effect. As described above flight segments were classified as 'homing' for displaced animals that had not yet returned to the roost, and as 'non-homing' for reference animals, and for displaced animals that had already returned to the roost of capture. We then determined whether or not the end point of each flight segment was a location that an individual had previously visited. It is important to note that other flight segments may also have ended at a point that the flying-fox had previously visited while they were not being tracked. We then repeated the above analyses, this time comparing metrics for flight segments that ended at a point that the animal was known to have visited before vs flight segments that did not. Speed, height above ground, and length were modelled with linear mixed effects models. Straightness index was modelled using the R package TMBglmm with a beta family, and orientation was modelled using a binomial generalised linear effects model where 'oriented' was defined as a flight segment \geq 99% oriented. Explanatory variables were considered significant if the model containing the variable of interest was <2 AICc from that of the null model, and if the p-value of the variable of interest was < 0.05. We used linear mixed effects models to examine the relationship between flight speed and height and height and straightness across all flight segments, while accounting for the length of each flight path. To account for repeated measures, 'individual' was included as a random factor. We used windspeed data (obtained from the Bureau of Meteorology (BoM) Kent Town weather station (-34.9° S, 138.6° E; located 1.91 km from the Adelaide roost and 16.6 km from the release site)) to examine whether windspeed may have affected ground speed. Mean windspeed ranged from 2.1 to 11.0 km/h, and maximum wind gust speed varied from 2.9 to 14.4 km/h across the six nights when movement paths were recorded. These maximum wind gust speeds are designated as 'force 2' ('light breeze') and 'force 3' ('gentle breeze'), respectively, on the Beaufort Scale [61] and as such are unlikely to have affected the flying-foxes' flight paths; therefore, windspeed was not included in the models.

Results

Tracking data

Displaced animals (n=11): Useful tracking data were obtained from 8 trackers, for a mean of 43.0 h (range 27.1–61.0 h, Supplementary Table 1). Of the remaining three trackers, one only logged positional information for 40 min, one did not log any data but was detected by another tracker at the roost, and the final tracker was last detected close to the release site.

Reference animals (n=7): Tracking data were obtained from 5 trackers for a mean of 83.5 h (range 36.7–143.2 h, Supplementary Table 1), though data from tracker $#506_R$ contained many missing points and could not be analysed. No data were obtained from the remaining two trackers (though individuals were confirmed to be present at the roost), and we assume they were faulty.

Homing times

Ten out of the 11 (91%) displaced flying-foxes were detected at the capture location within 4 days. Six of these returned to the roost within 25 h of release $(mean = 21.27 \pm 1.64 \text{ SE hrs}; range 16.08 - 24.83 h), includ$ ing one flying-fox (#981 $_{\rm D}$) for which tracking data were not obtained, but which was detected at the roost by another GPS logger (Supplementary Table 1). Two displaced flying-foxes were detected at the roost two days after release ($493_D \& 943_D$); one three days after release (913_D); and one four days after release (942_D). The final displaced flying-fox (517_D) was not detected within 7 days of release, it may have returned to the roost after this time, or the tracker may have fallen off prematurely, but this could not be confirmed. Of the eight tracked, displaced, individuals, full homing paths were obtained from five individuals. The remaining three displaced individuals did not return to the roost before the voltage of their GPS loggers became too low to log data; these animals were tracked for a mean of 42.48 ± 13.03 SE hours (range 37.51-47.98 h), and all three roosted at a second (different) location away from the roost of capture (Fig. 1; Supplementary Fig. 2; Supplementary Table 2). Despite no longer logging positional locations, these trackers were able to communicate with the base station at the roost, and thus the GPS position data already collected could still be obtained [47].



-34.84-

ш

-34.86

-34.88

-34.90

-34.90

-35.0 Latitude



-34.80 -

∢

34.90

-35.00

34.7 34 8

At the time of the experiments, flying-foxes returned to the Adelaide Botanic Park roost between 05:06 am and 07:14 am (fly-in detected using BoM radar data, following [62]; Supplementary Fig. 3); thus, the focal animals used for the homing experiment had 2-3.25 h available to fly the straight-line distance of 16.8 km back to the roost before fly-in ended. However, all displaced animals for which useful tracking data were obtained (n=8)roosted near the site of release (range: 58-1,912 m from the release site; Fig. 1; Supplementary Fig. 2; Supplementary Table 2) during the day following release. All of these animals departed from their individual day-time roost site between 17:41 and 18:54 (local time) on the evening of the day of release, broadly coinciding with the fly-out at the Adelaide Botanic Park roost detected using BoM radar data (c. 18:12–18:48; Supplementary Fig. 3 A-C).

Orientation

When the movement paths were tested for orientation, we found that of the five individuals for which full homing paths were obtained (#439_D, #474_D, #765_D, #785_D, #976_D) four were significantly oriented for the majority of their homeward flight (71–100% oriented; Supplementary Fig. 1; see 'orientation' in methods) with all nonoriented segments occurring in the early portion of their homing path (#439_D, #474_D, #785_D and #976_D; Fig. 2). The final flying-fox for which a complete movement path was obtained was not oriented at the beginning and the middle of its movement path (#765_D; Fig. 2), and was only oriented for the remaining 48% of its journey.

For four of the displaced flying-foxes for which full homing paths were obtained (#439_D, #785_D, #976_D, #765_D) further flights were recorded after they returned to the roost. Three of these (#439_D, #785_D, #976_D) were 100% oriented, whereas $#765_D$ landed at the Adelaide roost and then flew a short, tortuous path around the roost. Of the three displaced flying-foxes that spent two or more nights away from the roost (#493_D, #913_D, #943_D), one remained very close to the release site, and was oriented for 33% of the flight path that was long enough to be analysed (#493_D; Fig. 2); the remaining two displaced flying-foxes (#913_D, #943_D; Fig. 2) were unoriented in the middle of their recorded journeys and on average were oriented for 49% and 73% of their movement paths.

Of the reference flying-foxes for which paths could be analysed ($\#318_R$, $\#939_R$, $\#947_R$, $\#1006_R$), the majority of movement paths were oriented (68-97%), though each animal exhibited movement paths that were less than 60% oriented. Of these 'unoriented' movement paths the two by $\#318_R$ led from a roost site (away from the roost of capture) to two foraging sites; the one by $\#939_R$ seemed to involve circling at the roost before flying to a foraging location, the one by $#947_{\rm R}$ was a path from a foraging site to a roost site away from the roost of capture; and the one by $#1006_{\rm R}$ was between two foraging sites.

Flight metrics

The distance travelled and the number of stops greater than 10 min were calculated for each individual, for each night that complete flight paths were obtained. This resulted in 20 nights of data across 11 individuals. Nights were separated into 'homing' nights; which consisted of those of displaced animals that had not yet returned to the roost of capture (n=10; male=2, female=8) and 'non-homing' nights which consisted of those of reference animals, and of displaced animals that had returned to the roost of capture the previous night (n=10;male = 9, female = 1). We found that complete flight paths were significantly longer on 'homing' than 'non-homing' nights (Fig. 3A, 'homing': mean = $30,734 \text{ m} \pm 3,514$ SE; 'non-homing': mean = 11,578 m \pm 1,722 SE; Estimate = -14,167.7, F = 9.6, p = 0.006). When we examined the number of stops in a night, we found that there were significantly more stops on 'homing' than 'non-homing' nights (Fig. 3B, 'homing': mean = 5.1 ± 0.6 SE; 'nonhoming': mean = 3.0 ± 0.6 SE; Estimate = -0.53, F = 5.3, p = 0.02).

Flight metrics were calculated for 94 flight segments across all animals. We found that 'homing' flight segments (defined as those of displaced animals that had not yet returned to the roost of capture; n = 50; male = 9; female = 41) were significantly less likely to be oriented $(\text{mean} = 69\% \pm 5 \text{ SE vs. } 89\% \pm 4 \text{ SE}, \text{ Estimate} = -1.29,$ F = 5.08, p < 0.026; Fig. 4), were higher (mean = 35.7 ± 2.96 SE vs. 20.8 ± 2.25 SE, Estimate = 15.16, F = 14.5, p = 0.001; Fig. 4), and longer (mean = 6068.6 ± 695.9 SE vs. 3767.1 ± 370.9 SE, Estimate = 2257.9, F = 6.19, p = 0.021; Fig. 4), than 'non-homing' flight segments (defined as those of reference animals or displaced animals that had already returned to the roost of capture; n = 44; male = 32; female = 12), but there was no significant difference in ground speed (mean = 9.00 ± 0.20 SE vs. 8.46 ± 0.17 SE, $\Delta AIC < 2$; Fig. 4), or straightness (mean = 0.61 ± 0.04 SE vs. 0.73 ± 0.03 SE, $\triangle AIC < 2$; Fig. 4).

When we compared flight segments that were known to end in a location the animal had visited previously (n=23; male=12; female=11) to those that did not (n=71; male=29; female=42), we found that the former were significantly more likely to be oriented (mean= 8.95 ± 0.20 SE vs. 8.47 ± 0.17 SE, Estimate=1.6, F=5.46, p=0.018; Fig. 5), were faster (mean= 9.45 ± 0.29 SE vs. 8.52 ± 0.15 SE, Estimate=1.07, F=12.35, p<0.001; Fig. 5), straighter (mean= 0.80 ± 0.04 SE vs. 0.62 ± 0.03 SE, Estimate=0.73, z=2.967, p=0.003; Fig. 5), and higher (mean= 33.2 ± 4.91 SE vs. 27.4 ± 2.17 SE, Estimate=9.52,



Fig. 2 Plots showing whether the movement paths of each individual grey-headed flying-fox are oriented (red) or not oriented (black). The location of the Botanic Garden colony and release location are indicated where appropriate. Tracks are broken up into segments based on where the animals stopped for more than 10 min, black dots mark the beginning of each flight segment. Tracker identity is shown at the top of each plot, subscript D indicates displaced individuals, R indicates reference individuals. Movement paths shorter than 1 km, and movement paths without a known starting or end point were not analysed



Fig. 3 Box plots showing the distribution of values A total distance flown in a night, and **B** number of stops longer than 10 min in a night for 'homing nights' (n = 10) and 'non-homing nights' (n = 10). Only nights for which complete data was available were used. Nights were classified as 'homing' for displaced animals that had not yet reached the roost of capture and 'non-homing' if the individual had either been released at the roost (reference animals) or had roosted at the roost of capture the previous day (displaced animals)

F = 4.00, p = 0.048; Fig. 5), but there was no significant difference in length between flight segments that did and did not end at a point that the individual was known to have visited previously (mean = $5,506 \text{ m} \pm 692 \text{ SE}$ vs. $4,857 \pm 508$ SE, Estimate = 1133.48, F = 1.31, p = 0.254; Fig. 5).

Across all flight segments speed was significantly positively correlated with flight height above ground (Estimate = 0.05, t = 10.10, p < 0.001; Supplementary Table 3; Supplementary Fig. 5 A), and height above ground was significantly positively correlated with straightness index (Estimate = 26.10, t = 3.639, p < 0.001; Supplementary Table 3; Supplementary Fig. 5 B).

Discussion

We found that 10 of 11 grey-headed flying-foxes that had been displaced by16.8 km returned to the roost of capture within four days. The observed return rate is similar to that of two other studies where un-manipulated microbats were released at similar distances (<20 km), with a similar methodology [15, 63], and these rates are generally much higher than those of earlier studies where return rates were determined by sighting individuals at the roost of capture [see 64 for a review]. We separated flight paths of displaced animals into pre- and post- return to the roost of capture and labelled them as 'homing' and 'non-homing' we also examined the non-homing flights of seven 'reference' flying-foxes released at the roost of capture. We found that the distance flown on 'homing' nights was almost three times longer than the distance flown on 'non-homing' nights. When we examined flight metrics of 'homing' vs 'non-homing' flight segments, we found that 'homing' flight segments were significantly higher, longer, and less likely to be oriented than 'non-homing' flight segments. In addition, flight segments that ended in a location that the animal was known to have visited before were significantly higher, faster, straighter, and more likely to be oriented than segments that ended in a location that the animal was not known to have visited previously. Overall, the findings are consistent with the idea that flying-foxes may use a large-scale navigational map based on vision, but further studies involving sensory manipulation would be required to confirm this.

None of the displaced animals returned directly to the roost of capture after release, which was contrary to our expectations; all animals were given fruit juice before release and provision of food has previously been shown to facilitate an animal's direct return to the roost [4], in addition all animals were released relatively late in the night to increase their motivation to return 'home' rather than to forage. It is possible, though, that the animals were released too late in the night and may have homed directly if released earlier. Most animals were released c. 5:00 am and according to BoM radar data [62] (Supplementary Fig. 3) flying-foxes began to return to the roost around this time, and fly-in ended at c. 7:14 am. This left a maximum of 2 h for the flying-foxes to return to the roost of capture. We know that roosting alone is common in similar species [65-71], and has an ecdotally been observed many times previously in the grey-headed flying-fox [72, 73], which suggests that the costs of roosting alone are likely to be minimal. Indeed, two of the tracked flying-foxes that were released at the roost (n=7) also roosted away from the roost for two nights, (Supplementary Table 2; Fig. 1; Supplementary Fig. 2). Thus, roosting away from the roost of capture may not be indicative of being 'lost'.

When we examined the distance flown between 'homing' and 'non-homing' nights however, we found that displaced individuals that had not yet returned to the roost of capture on average flew almost three times farther than reference animals, or displaced animals that had returned to the colony the previous day. It is important



Fig. 4 Box plots showing the distribution of values for five flight metrics calculated for homing, and non-homing flight segments, means are shown as red dots. Flight segments were classified as 'homing' for displaced animals that had not yet reached the roost of capture and 'non-homing' if the individual had either been released at the roost (reference animals) or had roosted at the roost of capture the previous day (displaced animals)

to note however, that there is a highly skewed sex ratio between the 'homing' and 'non-homing' nights. This is because the reference individuals were part of a separate study targeting male flying-foxes. This resulted in most 'homing' nights (8/10) being performed by females, and the majority of 'non-homing' nights being performed by males (9/10). Our previous work [38] suggests that female grey-headed flying-foxes fly further when foraging than males. However, the magnitude of the difference in distance flown between 'homing' and 'non-homing' nights is much greater than that of females vs males in our previous study (i.e. homing flights are a mean of 2.65 times longer in this study, vs a mean of 1.35 times longer in major urban areas in our previous study [38]). In addition, the male 'homing' paths were longer than any male 'non-homing' paths, and the female 'non-homing' path is shorter than any of the female 'homing' paths. Also, importantly, the two displaced animals that roosted away from the roost of capture for an additional night $(493_D \&$ $943_{\rm D}$) flew similarly long distances on their second 'displaced night' as did the displaced animals that returned to the roost. This suggests that these individuals were attempting to return to the roost of capture, rather than choosing to roost in a new location. It is difficult, however, to disentangle whether these animals may have had to fly greater distances because they were attempting to find food resources in an unknown area, or whether they were attempting to locate the roost of capture. In future studies this uncertainty could be reduced by increasing an individuals' motivation to home.

Motivation to home is an important factor in homing studies, for example, it has been shown that homing pigeons, the model species for which a large amount of bird navigation research is based, have been selectively bred for an increased homing drive, rather than an increase in homing ability [74]. A high motivation to home means that the results of homing experiments are easier to interpret, as a lack of return is likely to reflect an inability to return to the goal rather than a reduced motivation to do so. There are times of the year where the motivation to home could be increased for social species such as the grey-headed flying-fox, for example, from March-mid April when sexual activity is highest [42] large adult males are likely to hold mating territories containing a harem [41], and therefore would likely be more motivated to return to the roost to protect their reproductive interests [75]. Similarly, in January and February most females have left dependant young in the roost [76] and therefore would likely be highly motivated to return,



Fig. 5 Box plots showing the distribution of values for five flight metrics calculated for flight segments ending at points the individual was known to have previously visited (known, n = 23), or not known to have previously visited (unknown, n = 71)

but any displacement experiment capitalizing on this would have major ethical implications.

Tracking data show that individual grey-headed flyingfoxes traverse vast distances throughout their extensive species range (from Rockhampton in Queensland to Adelaide in South Australia [76, 77]) on an annual basis [8], visiting an average of 18 different roost sites per year among a network of several hundred known roosts [8, 38, 78]. This extreme mobility suggests that these animals are likely to have sophisticated navigation abilities; however, it is possible that different navigation systems are used when navigating over vast continental-scale distances versus the relatively short distances used in this study. For example, large scale maps, such as magnetic [12] or olfactory [20] maps as have been suggested for bat navigation, might be too coarse to be useful over a short distance. Recent GPS tracking of Egyptian fruit bats shows that these animals can perform large-scale map based navigation by relying on visual features [19]. Unlike a map based on the geomagnetic field or olfaction, a map based on visual features is in theory only useful if these visual features are familiar. Grey-headed flying-foxes are known to forage at sites up to 75 km from their day roost [29, 52, 79], so it is therefore possible that the release site would have been close to an area with which an animal has had direct sensory contact [80] for most individuals used in this study. This suggests that the individuals in this study could have used familiar landmarks to orient themselves with respect to the home goal, although any familiar visual landmarks may not have been apparent to the animals straight away upon release. It is possible that the lights of the city of Adelaide, or the skyglow emanating from these lights from beyond the horizon, may have acted as a familiar or attractive visual feature that could have been detected from a distance [81], potentially even from, or close to, the release site, once the animals were airborne. It has been shown that skyglow is attractive to migratory birds [82], and it has been suggested that city lights may be important for bat homing [4].

When metrics of individual flight segments were examined, we found that 'homing' flight segments were less likely to be oriented but were higher and longer than 'non-homing' flight segments (those of reference individuals or displaced individuals that had already returned to the roost of capture), suggesting that when individuals were unaware of where they were relative to their goal they may have flown higher, possibly in an attempt to gain line of sight of distant landmarks to orient themselves. In contrast, when flight segments that ended at a point that individuals were known to have visited previously were compared to flight segments that did not end at a point they were previously known to have visited, flight segments were more likely to be oriented and were faster and straighter, but were also higher, suggesting that when individuals were aware of where they were relative to their goal, they sought to reach their goal using the fastest, most direct route possible [e.g. 4]. We also found a significant positive correlation between flight height and speed (Supplementary Fig. 5A), with lower flights being slower, so it is possible that when an individual is oriented towards a goal it flies higher and faster, but when it is e.g. trying to identify new food sources it might fly lower and at slower speeds. This ties in with the significant correlation we found between flight height, and straightness index, where lower flights were associated with lower straightness indexes (Supplementary Fig. 5B).

In this study we found some tracks that appeared to follow linear features for short distances in four tracked individuals (Supplementary Fig. 4). Linear features have been shown to provide visual information that can influence dispersal and navigation of aerial animals [83–87]. Pigeons that are highly familiar with a homing route have been shown to selectively follow linear features that are oriented in the home direction [88]; but linear features have also been shown to be important for animals less familiar with the landscape [e.g. 83, 89]. A recent study of grey-headed flying-foxes roosting at the same site, the Adelaide Botanic Park roost, identified instances of individual's flight paths aligning with roads and rivers [37]. It has been suggested that linear feature following may reduce the number of waypoints (landmarks) that an individual needs to remember, and therefore reduces cognitive load [88]. It is possible that when an animal is unfamiliar with an area, linear feature following may aid navigation by allowing animals to explore the landscape while providing a cognitively simple way to return to their starting point. In our study, a prominent linear feature, the River Torrens, used by an individual in Boardman et al. [37], approximately aligns with the homeward direction from the release site (see Fig. 1; Figure S1 [37]). While this river does not seem to have had a major influence on the subjects in our present study, the final, oriented, paths of $\#785_{\rm D}$ and $\#976_{\rm D}$ aligned broadly with the river-though they do not follow the twists and turns of the river, it is likely that the animals would have been able to see the river whilst flying.

Conclusion

We showed that arboreally roosting flying-foxes displaced to a site 16.8 km from the roost of capture were able to return to the roost of capture 1–4 days following release. All animals roosted away from the colony for at least one night, and some for multiple nights. While it seems that roosting alone is a relatively frequent occurrence, the fact that displaced animals flew on average almost three times further in a night than individuals that were not displaced suggests that these animals were attempting to return to the roost of capture. The possibility of low motivation to 'home' makes it difficult for the results of this study to be interpreted. Future studies should address this issue, and crucially should include sensory manipulations such as influencing flying-foxes' access to potential compass cues such as celestial cues via release under cloudy versus clear nights [90], or magnetic cues via release with and without on-board magnets [87, 91], or examining the influence of lighting on movement, in order to further improve our understanding of bat navigation.

Supplementary Information

The online version contains supplementary material available at https://doi. org/10.1186/s40462-025-00532-x.

Additional file 1.

Acknowledgements

We thank Terry Reardon and University of Adelaide volunteers for assistance in catching flying-foxes; Ian Smith, Dianne Hakoff, Jenny and David McLelland, Rebecca Probert and others at Adelaide Zoo for providing the equipment and space; and Kathy Burbidge for help with processing flying-foxes. We thank Jim McLean for valuable discussion about the analysis.

Author contributions

JM conceived the project, JM and JAW designed the study. JM, JMM, MJW, CT, WSJB, & AM conducted fieldwork. JM analysed the data and drafted the manuscript. All authors contributed to reviewing and editing the manuscript. All authors read and approved the final manuscript.

Funding

JM, CT, MJW & JAW were supported by an Australian Research Council (ARC) Discovery Grant (DP170104272).

Availability of data and materials

The dataset analysed during the current study are available on reasonable request.

Declarations

Ethics approval and consent to participate

All aspects of fieldwork were approved by Western Sydney University Animal Research Authority no. A12217 and SA Department for Environment and Water permit to undertake scientific research M26735.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Author details

¹ Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW 2753, Australia. ²Ecological Consulting, Ecosure, Fortitude Valley, QLD 4006, Australia. ³Commonwealth Scientific and Industrial Research Organisation (CSIRO), Land and Water, Waite Rd, Urrbrae, SA 5064, Australia. ⁴School of Science, Western Sydney University, Penrith, NSW 2751, Australia. ⁵School of Life and Environmental Sciences, Faculty of Science, Engineering and Built Environment, Deakin University, Burwood, VIC 3125, Australia. ⁶Department of Pathobiology and Population Health, School of Animal and Veterinary Sciences, University of Adelaide, Roseworthy, SA 5371, Australia. Received: 28 August 2024 Accepted: 8 January 2025 Published online: 25 March 2025

References

- Bingman VP, Cheng K. Mechanisms of animal global navigation: comparative perspectives and enduring challenges. Ethol Ecol Evol. 2005;17(4):295–318.
- Cvikel N, Berg KE, Levin E, Hurme E, Borissov I, Boonman A, et al. Bats aggregate to improve prey search but might be impaired when their density becomes too high. Curr Biol. 2015;25(2):206–11.
- Sapir N, Horvitz N, Dechmann DK, Fahr J, Wikelski M. Commuting fruit bats beneficially modulate their flight in relation to wind. Proc R Soc B Biol Sci. 2014;281(1782):20140018.
- Tsoar A, Nathan R, Bartan Y, Vyssotski A, Dell'Omo G, Ulanovsky N. Large-scale navigational map in a mammal. Proc Natl Acad Sci. 2011;108(37):E718–24.
- 5. Griffin DR. Migrations and homing of bats. Biol Bats. 2012;233:56.
- 6. Richter H, Cumming G. First application of satellite telemetry to track African straw-coloured fruit bat migration. J Zool. 2008;275(2):172–6.
- Bisson I-A, Safi K, Holland RA. Evidence for repeated independent evolution of migration in the largest family of bats. PLoS ONE. 2009;4(10): e7504.
- Welbergen JA, Meade J, Field HE, Edson D, McMichael L, Shoo LP, et al. Extreme mobility of the world's largest flying mammals creates key challenges for management and conservation. BMC Biol. 2020;18(1):1–13.
- Tidemann CR, Nelson JE. Long-distance movements of the grey-headed flying fox (*Pteropus poliocephalus*). J Zool. 2004;263(2):141–6.
- Holland RA. Orientation, navigation and homing in bats. In: Choe JC, editor. Encyclopedia of animal behavior, (2nd ed). 3: Elsevier: Academic Press; 2019. p. 611–21.
- 11. Emlen ST, Emlen JT. A technique for recording migratory orientation of captive birds. Auk. 1966;83(3):361–7.
- Baerwald EF, Weller TJ, Green DM, Holland RA. There and back again: homing in bats revisited. 50 Years of Bat Research. Berlin: Springer; 2021. p. 173–87.
- Holland RA, Kirschvink JL, Doak TG, Wikelski M. Bats use magnetite to detect the earth's magnetic field. PLoS ONE. 2008;3(2): e1676.
- Holland RA, Borissov I, Siemers BM. A nocturnal mammal, the greater mouse-eared bat, calibrates a magnetic compass by the sun. Proc Natl Acad Sci. 2010;107(15):6941–5.
- Holland RA, Thorup K, Vonhof MJ, Cochran WW, Wikelski M. Navigation: bat orientation using Earth's magnetic field. Nature. 2006;444(7120):702.
- Wang Y, Pan Y, Parsons S, Walker M, Zhang S. Bats respond to polarity of a magnetic field. Proc R Soc B Biol Sci. 2007;274(1627):2901–5.
- 17. Greif S, Borissov I, Yovel Y, Holland RA. A functional role of the sky's polarization pattern for orientation in the greater mouse-eared bat. Nat Commun. 2014;5(1):1–4.
- Childs S, Buchler E. Perception of simulated stars by *Eptesicus fuscus* (Vespertilionidae): a potential navigational mechanism. Anim Behav. 1981;29(4):1028–35.
- Harten L, Katz A, Goldshtein A, Handel M, Yovel Y. The ontogeny of a mammalian cognitive map in the real world. Science. 2020;369(6500):194–7.
- Genzel D, Yovel Y, Yartsev MM. Neuroethology of bat navigation. Curr Biol. 2018;28(17):R997–1004.
- Safi K, Dechmann DK. Adaptation of brain regions to habitat complexity: a comparative analysis in bats (Chiroptera). Proc R Soc B Biol Sci. 2005;272(1559):179–86.
- Jacobs LF. From chemotaxis to the cognitive map: the function of olfaction. Proc Natl Acad Sci. 2012;109(Supplement 1):10693–700.
- Reep R, Finlay B, Darlington R. The limbic system in mammalian brain evolution. Brain Behav Evol. 2007;70(1):57–70.
- Aziz SA, McConkey KR, Tanalgo K, Sritongchuay T, Low M-R, Yong JY, et al. The critical importance of Old World fruit bats for healthy ecosystems and economies. Front Ecol Evol. 2021;9:181.
- NSW Scientific Committee. Grey-headed flying-fox—vulnerable species listing. Sydney, NSW: NSW Scientific Committee. https:// www.2environmentnswgovau/topics/animals-and-plants/threatenedspecies/nsw-threatened-species-scientific-committee/determinations/

- 26. Eby P, Roberts B, Pennay M, Welbergen J. *Pteropus poliocephalus*. The IUCN Red List; 2021.
- 27. Roberts BJ, Mo M, Roache M, Eby P. Review of dispersal attempts at flyingfox camps in Australia. Aust J Zool. 2021;6:66.
- Roberts BJ, Catterall CP, Eby P, Kanowski J. Long-distance and frequent movements of the flying-fox *Pteropus poliocephalus*: implications for management. PLoS ONE. 2012;7(8): e42532.
- 29. Eby P. Seasonal movements of grey-headed flying-foxes, *Pteropus poliocephalus* (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. Wildl Res. 1991;18(5):547–59.
- 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(2):204–12.
- Mildenstein TL, Stier SC, Nuevo-Diego C, Mills LS. Habitat selection of endangered and endemic large flying-foxes in Subic Bay. Philipp Biol Conserv. 2005;126(1):93–102.
- 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.
- 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.
- Nakamoto A, Kinjo K, Izawa M. Ranging patterns and habitat use of a solitary flying fox (*Pteropus dasymallus*) on Okinawa-jima Island, Japan. Acta Chiropterologica. 2012;14(2):387–99.
- Weber N, Duengkae P, Fahr J, Dechmann DK, Phengsakul P, Khumbucha W, et al. High-resolution GPS tracking of Lyle's flying fox between temples and orchards in central Thailand. J Wildl Manag. 2015;79(6):957–68.
- Fahr J, Abedi-Lartey M, Esch T, Machwitz M, Suu-Ire R, Wikelski M, Dechmann DK. Pronounced seasonal changes in the movement ecology of a highly gregarious central-place forager, the African straw-coloured fruit bat (*Eidolon helvum*). PLoS ONE. 2015;10(10):66.
- Boardman WS, Roshier D, Reardon T, Burbidge K, McKeown A, Westcott DA, et al. Spring foraging movements of an urban population of grey-headed flying foxes (*Pteropus poliocephalus*). J Urban Ecol. 2021;7(1):juaa034.
- Meade J, Martin JM, Welbergen J. Fast food in the city? Nomadic flyingfoxes commute less and hang around for longer in urban areas. Behav Ecol. 2021;32(6):1151–62.
- Benhamou S. Detecting an orientation component in animal paths when the preferred direction is individual-dependent. Ecology. 2006;87(2):518–28.
- Nelson J. Movements of Australian flying foxes (Pteropodidae: Megachiroptera). Aust J Zool. 1965;13(1):53–74.
- 41. Welbergen JA. The social organisation of the grey-headed flying-fox, *Pteropus poliocephalus*. Cambridge: University of Cambridge; 2005.
- 42. Welbergen JA. Fit females and fat polygynous males: seasonal body mass changes in the grey-headed flying fox. Oecologia. 2011;165(3):629–37.
- Eby P. The biology and management of flying foxes in NSW. NSW National Parks and Wildlife Service; 1995.
- Nelson JE. Behaviour of Australian pteropodidae (Megacheroptera). Anim Behav. 1965;13(4):544–57.
- Welbergen J. Growth, bimaturation, and sexual size dimorphism in wild gray-headed flying foxes (*Pteropus poliocephalus*). J Mammal. 2010;91(1):38–47.
- Jonsson N, Johnston S. Field anaesthesia of three Australian species of flying fox. Vet Rec. 2004;154(21):664.
- Jurdak R, Sommer P, Kusy B, Kottege N, Crossman C, Mckeown A, Westcott D, editors. Camazotz: multimodal activity-based GPS sampling. In: Proceedings of the 12th international conference on information processing in sensor networks; 2013: ACM.
- De Jong C, Field H, Tagtag A, Hughes T, Dechmann D, Jayme S, et al. Foraging behaviour and landscape utilisation by the endangered golden-crowned flying fox (*Acerodon jubatus*), the Philippines. PLoS ONE. 2013;8(11): e79665.
- Turbill C, Walker M, Boardman W, Martin JM, McKeown A, Meade J, Welbergen JA. Torpor use in the wild by one of the world's largest bats. Proc R Soc B. 2026;2024(291):20241137.

- Walker MJ. Thermoregulatory physiology, energetics, and behaviour of free-living grey-headed flying-foxes, Pteropus poliocephalus, in response to natural variation in thermal conditions [PhD]. Western Sydney University; 2022.
- Todd CM, Westcott DA, Martin JM, Rose K, McKeown A, Hall J, Welbergen JA. Body-size dependent foraging strategies in the Christmas Island flying-fox: implications for seed and pollen dispersal within a threatened island ecosystem. Mov Ecol. 2022;10(1):19.
- Field HE, Smith CS, de Jong CE, Melville D, Broos A, Kung N, et al. Landscape utilisation, animal behaviour and Hendra virus risk. EcoHealth. 2016;13(1):26–38.
- Gupte PR, Beardsworth CE, Spiegel O, Lourie E, Toledo S, Nathan R, Bijleveld Al. A guide to pre-processing high-throughput animal tracking data. J Anim Ecol. 2022;91(2):287–307.
- Carpenter RE. Flight physiology of flying foxes, *Pteropus poliocephalus*. J Exp Biol. 1985;114(1):619–47.
- 55. Ratcliffe F. Notes on the fruit bats (Pteropus spp.) of Australia. J Anim Ecol. 1932;66:32–57.
- 56. R Core Team. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing; 2021.
- 57. RStudio Team. RStudio: integrated development environment for R. Boston, MA RStudio, PBC; 2021.
- Girard C, Benhamou S, Dagorn L. FAD: fish aggregating device or fish attracting device? A new analysis of yellowfin tuna movements around floating objects. Anim Behav. 2004;67(2):319–26.
- 59. Bovet P, Benhamou S. Spatial analysis of animals' movements using a correlated random walk model. J Theor Biol. 1988;131(4):419–33.
- 60. McLean DJ, Skowron Volponi MA. trajr: an R package for characterisation of animal trajectories. Ethology. 2018;124(6):440–8.
- 61. Forrester FH. How strong is the wind? The origin of the Beaufort Scale. Weatherwise. 1986;39(3):147–51.
- Meade J, Van der Ree R, Stepanian PM, Westcott DA, Welbergen JA. Using weather radar to monitor the number, timing and directions of flyingfoxes emerging from their roosts. Sci Rep. 2019;9(1):1–10.
- 63. Guilbert J, Walker M, Greif S, Parsons S. Evidence of homing following translocation of long-tailed bats (*Chalinolobus tuberculatus*) at Grand Canyon Cave, New Zealand. N Zeal J Zool. 2007;34(3):239–46.
- 64. Davis R. Homing performance and homing ability in bats. Ecol Monogr. 1966;36(3):201–37.
- 65. Wiles G. Current research and future management of Marianas fruit bats (Chiroptera: Pteropodidae) on Guam. Aust Mammal. 1987;10:93–5.
- 66. Cox PA. Observations on the natural history of Samoan bats; 1983.
- 67. Cheke A, Dahl J. The status of bats on western Indian Ocean islands, with special reference to Pteropus. 1981.
- Phillips W. A note on the flying fox (*Pteropus hypomelanus maris*) of Addu Atoll, Maldive Islands. J Bombay Nat Hist Soc. 1958;55:334–7.
- 69. Goodwin RE. The bats of Timor: systematics and ecology. Am Museum Nat Hist. 1979;6:66.
- McKean JL. Notes on some collections of bats (order Chiroptera) from Papua-New Guinea and Bougainville Island. Melbourne: CSIRO; 1972.
- 71. Bruner P, Pratt H. Notes on the status and natural history of Micronesian bats. Elepaio. 1979;40(1):1–4.
- Mo M, Meade J, Price J, Maisey J, Welbergen JA. Synchronous abortion events in the grey-headed flying-fox (*Pteropus poliocephalus*). Pac Conserv Biol. 2022;29(2):110–8.
- Mo M. Going it alone: observations of solitary roosting in two Australian flying-foxes (*Pteropus alecto* and *P. poliocephalus*). Australian Mammalogy. 2024;46(3).
- Visalberghi E, Foa A, Baldaccini N, Alleva E. New experiments on the homing ability of the rock pigeon. Monitore Zoologico Italiano Ital J Zool. 1978;12(2–3):199–209.
- Klose SM, Welbergen JA, Kalko EK. Testosterone is associated with harem maintenance ability in free-ranging grey-headed flying-foxes, *Pteropus poliocephalus*. Biol Lett. 2009;5(6):758–61.
- Baker A, Gynther I. Strahan's the mammals of Australia. New Holland Publishers; 2023.
- Currey K, Kendal D, Van der Ree R, Lentini PE. Land manager perspectives on conflict mitigation strategies for urban flying-fox camps. Diversity. 2018;10(2):39.

- Timmiss LA, Martin JM, Murray NJ, Welbergen JA, Westcott D, McKeown A, Kingsford RT. Threatened but not conserved: flying-fox roosting and foraging habitat in Australia. Aust J Zool. 2021;6:66.
- Yabsley SH, Meade J, Hibburt TD, Martin JM, Boardman WS, Nicolle D, et al. Variety is the spice of life: Flying-foxes exploit a variety of native and exotic food plants in an urban landscape mosaic. Front Ecol Evol. 2022;10: 907966.
- Wallraff HG. Navigation by homing pigeons: updated perspective. Ethol Ecol Evol. 2001;13(1):1–48.
- Falchi F, Cinzano P, Duriscoe D, Kyba CC, Elvidge CD, Baugh K, et al. The new world atlas of artificial night sky brightness. Sci Adv. 2016;2(6): e1600377.
- Horton KG, Buler JJ, Anderson SJ, Burt CS, Collins AC, Dokter AM, et al. Artificial light at night is a top predictor of bird migration stopover density. Nat Commun. 2023;14(1):7446.
- Brebner JS, Makinson JC, Bates OK, Rossi N, Lim KS, Dubois T, et al. Bumble bees strategically use ground level linear features in navigation. Anim Behav. 2021;179:147–60.
- Gesicki DV, Cech EL, Bingman VP. Detoured flight direction responses along the southwest coast of Lake Erie by night-migrating birds. The Auk. 2019;136(3):ukz018.
- Schiffner I, Wiltschko R. Pigeon navigation: different routes lead to Frankfurt. PLoS ONE. 2014;9(11): e112439.
- Guilford T, Roberts S, Biro D, Rezek I. Positional entropy during pigeon homing II: navigational interpretation of Bayesian latent state models. J Theor Biol. 2004;227(1):25–38.
- Meade J, Biro D, Guilford T. Homing pigeons develop local route stereotypy. Proc R Soc B Biol Sci. 2005;272(1558):17–23.
- Biro D, Meade J, Guilford T. Familiar route loyalty implies visual pilotage in the homing pigeon. Proc Natl Acad Sci. 2004;101(50):17440–3.
- Lipp H-P, Vyssotski AL, Wolfer DP, Renaudineau S, Savini M, Tröster G, Dell'Omo G. Pigeon homing along highways and exits. Curr Biol. 2004;14(14):1239–49.
- Moser El. A bat's perspective on navigation. Proc Natl Acad Sci. 2011;108(38):15665–6.
- Bonadonna F, Bajzak C, Benhamou S, Igloi K, Jouventin P, Lipp H, Dell'Omo G. Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance. Proc R Soc Lond B Biol Sci. 2005;272(1562):489–95.

Publisher's Note

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