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Optimal foraging in seasonal environments: implications for residency of Australian flying foxes in food-subsidized urban landscapes

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Bats provide important ecosystem services such as pollination of native forests; they are also a source of zoonotic pathogens for humans and domestic animals. Human-induced changes to native habitats may have created more opportunities for bats to reside in urban settings, thus decreasing pollination services to native forests and increasing opportunities for zoonotic transmission. In Australia, fruit bats (*Pteropus* spp. flying foxes) are increasingly inhabiting urban areas where they feed on anthropogenic food sources with nutritional characteristics and phenology that differ from native habitats. We use optimal foraging theory to investigate the relationship between bat residence time in a patch, the time it takes to search for a new patch (simulating loss of native habitat) and seasonal resource production. We show that it can be beneficial to reside in a patch, even when food productivity is low, as long as foraging intensity is low and the expected searching time is high. A small increase in the expected patch searching time greatly increases the residence time, suggesting nonlinear associations between patch residence and loss of seasonal native resources. We also found that sudden increases in resource consumption due to an influx of new bats has complex effects on patch departure times that again depend on expected searching times and seasonality. Our results suggest that the increased use of urban landscapes by bats may be a response to new spatial and temporal configurations of foraging opportunities. Given that bats are reservoir hosts of zoonotic diseases, our results provide a framework to study the effects of foraging ecology on disease dynamics.

One contribution of 14 to a theme isssue 'Anthropogenic resource subsidies and host–parasite dynamics in wildlife'.

1. Introduction

The aggregation of animals around food resources is an important driver of disease transmission [1] and spillover to new host species [2]. For many animals, food availability exhibits substantial seasonal and spatial variation. In particular, foods such as fruit and floral nectar occur in habitat patches with variable levels of synchrony across space. Animals that rely on such ephemeral resources must be highly mobile and must make decisions about the time spent exploiting a given food patch. Such decisions are probably based on the energetic profitability of the resources and the costs associated with finding a new food patch [3–9]. In human-modified landscapes, animals are confronted with new foraging conditions imposed by the removal of traditional food sources and/or the appearance of exotic foods with different nutritional and yield characteristics. Animals may respond to changes in the distribution, abundance and quality of food resources by adjusting their foraging strategies [10–12], which may explain

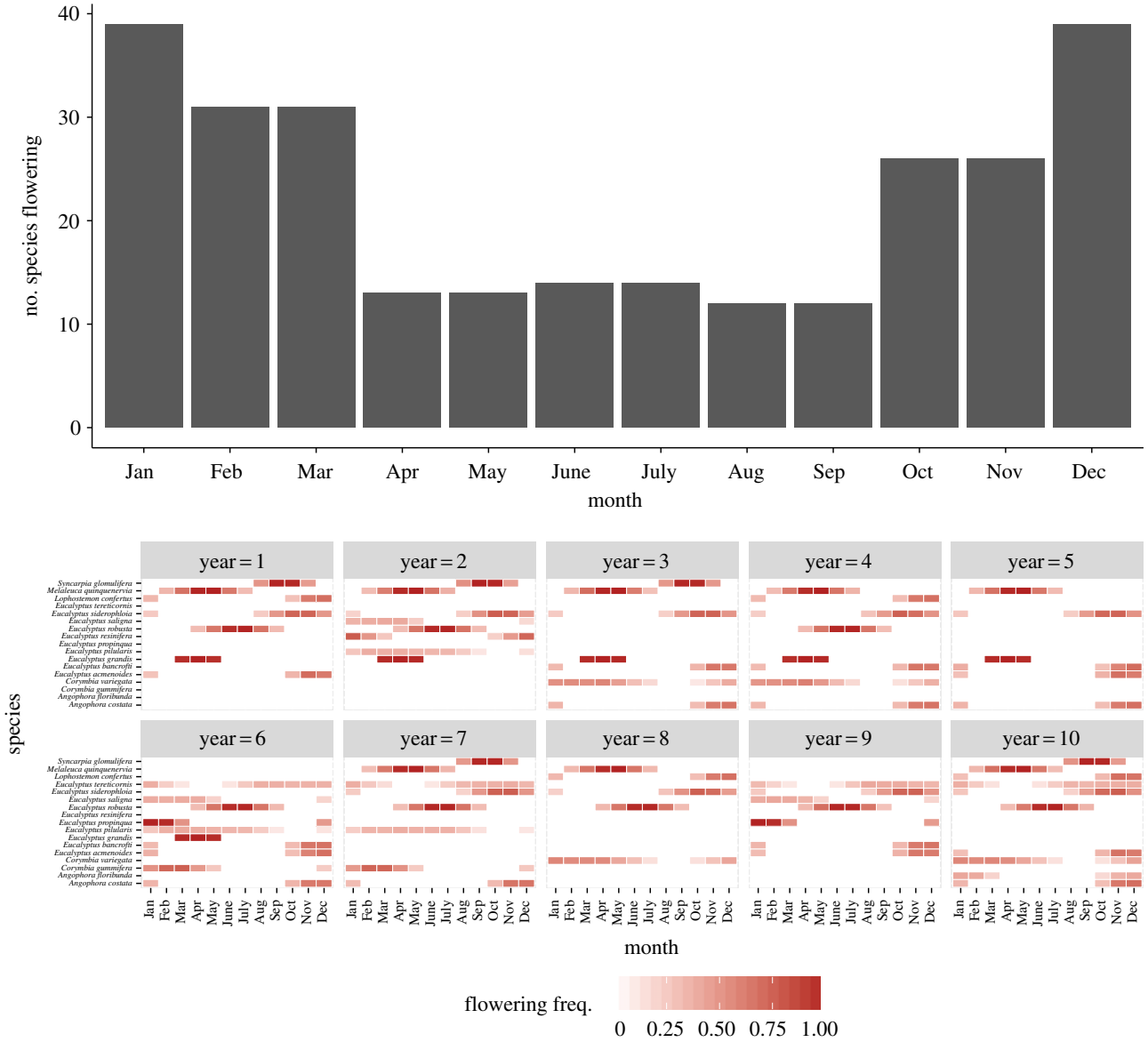

Figure 1. Irregular flowering patterns of flying fox food in subtropical Australia. (*a*) The maximum number of species flowering per month out of 56 species known to be nectar food sources for bats in New South Wales, Australia (adapted from [32]). (*b*) Simulation of the irregular flowering events of Eucalypt species over a 10-year period. This simulation was created by randomly drawing flowering events from flowering frequency data collected by Law *et al.* [31]. The figure illustrates that irregular flowering events can lead to occasional food bottlenecks.

why some foragers utilize urban habitats with increasing frequency and duration [13,14]. In the context of public health and animal welfare, this is important because the use of urban and peri-urban habitats by animals hosting zoonotic diseases increases the risk of disease spillover [15,16].

Evaluating the conditions that lead to increased patch residence time, such as the interplay between resource seasonality, habitat clearing and foraging decisions could thus provide valuable insights into the dynamics of animal-borne diseases [17,18]. For example, disease expression could depend on the foraging ecology of hosts because immune mechanisms of defence are energetically costly [19,20]. Similarly, among-hosts dynamics could depend on the foraging decisions made by host in different classes of infection [21,22].

Pteropodid bats across the world are known to be reservoir hosts of several diseases that may transmit to livestock and humans [16,23–25]. Previous work on Australian *pteropus* bat species (commonly named flying foxes) has shown that disease spillover is greater in areas where bats, livestock and humans co-inhabit [16,26,27]. Although urban Australian flying foxes are considered a nuisance and are often removed from urban settings, in most other countries, human–bat contact is facilitated by the valuable services that bats provide including bushmeat and guano (which serves as fertilizer). Elucidating the mechanisms that favour human–bat contact may thus be useful in the management of bat-borne viral diseases such as Ebola, Nipah and Hendra [23,25].

Australian flying foxes establish roosts near habitat patches where fruit and nectar are produced [28–30]. However, such food sources are spatially scattered because of variation in tree community composition and in the flowering phenology of any given tree species in space [31, see also figure 1]). Such asynchronous production of food and the dependence of flying foxes on high-energy-yielding food sources [31,32] is thought to explain the nomadic behaviour of flying foxes. However, the four species of flying foxes in Australia differ in their dietary requirements. In urban and peri-urban habitats, generalist species, such as *Pteropus alecto*, exploit a combination of native and exotic food sources [33–35], which may favour increased residency in urban habitats due to a constant food

supply across seasons [36]. Furthermore, longer residence time in urban landscapes could result from loss of native habitat across the landscape or from loss of habitat that flowers within specific seasons [30]. In either case, higher energetic demands would be required to find new habitat patches producing food [32]. It is thus possible that both the increased transit distance imposed by habitat clearing and a more constant food supply from non-native food items explain the increased time that some species of flying foxes spend near urban habitats. While patch residence times and the movement behaviour of flying foxes is affected by a multitude of factors, previous work suggests that flying foxes display optimal foraging behaviours in selecting roosting and foraging sites [37], so that patch residence time is at least partly guided by energetic considerations.

Our aim is to predict how seasonal fluctuation in resources and habitat fragmentation or patch isolation (measured as the expected time required to travel to a different patch) affect patch residence times of flying foxes. We assume that bats make optimal foraging decisions, such that the patch residence time depends on marginal energetic gains obtained through foraging in the patch with respect to expected energetic costs of finding a new patch. To help explain the increase in number of permanent flying fox camps near urban landscapes in Australia [38,39], we specifically seek to identify conditions that lead to longer residence times in habitats with lower amplitude of seasonal resource variation (i.e. more consistent resources). For cases of high seasonality, we then characterize the effect of initial food density at the time of bat arrival on the patch residence time. Finally, we quantify the effects of sudden immigration events associated with floral blooms on the patch residence time of established bats.

2. Material and methods

(a) Dynamic model

We built a dynamic model to track resource abundance $R(t)$ in a single patch and the amount of energy $E(t)$ stored by a colony of bats since their arrival at time $t = 0$ days. In the absence of bats, the resources (which can be nectar or fruit) are assumed to follow a logistic growth model [40], with resource birth ν and carrying capacity $K(t)$ that oscillates as a cosine function with a period (d) of one year between $1 + k_1$ (peak) and $1 - k_1$ (trough) in arbitrary units. The assumption of logistic growth of the resource is justified by the observation that nectar production is replenished following consumption [41]. Resources are also assumed to oscillate seasonally given that the flowering abundance of native tree species greatly decreases in winter (figure 1). Bat foraging occurs at constant rate β which implicitly captures the colony size, assuming that all bats arrive and leave at the same time. Bats convert the consumed resources into energy $E(t)$ at rate ϕ. While in the patch, bats consume energy at metabolic rate μ. When bats leave the patch, they expect to spend an arbitrary time T searching for and travelling to a new suitable patch, resulting in a net energy expenditure of cT. Note that we define a patch as encompassing both roosting and feeding sites within a close distance; this is in line with the observation that flying foxes forage in the vicinity of their roosting site and that migration to new roosts is correlated with the use of different foraging areas [42]. This leads to the following set of differential equations:

$$\frac{dR}{dt} = R\left[\nu\left(1 - \frac{R}{K(t)}\right) - \beta\right], \tag{2.1}$$

$$\frac{dE}{dt} = \phi\beta R - \mu E, \tag{2.2}$$

$$E(0) = 0, \tag{2.3}$$

$$\text{and} \quad K(t) = 1 + k_1 \cos(d2\pi t). \tag{2.4}$$

(b) Decision model

While patch occupancy and migration patterns of flying foxes have been shown to correlate with spatiotemporal variations in food abundance [28,43], the underlying decision process is poorly characterized. Here we consider one particular framework, known as the marginal value theorem [44], which has been used to model resource-driven migration behaviour in several animal taxa [45–48]. In short, the model assumes that the optimal residence time in a patch is the value that maximizes the net average energy gain $E^*(t)$: 'net' because we discount the energy spent travelling to the next patch (cT), and 'average' as we normalize by the sum of the residence and travelling times:

$$E^*(t) = \frac{E(t) - cT}{T + t}. \tag{2.5}$$

As shown by [44], and summarized in electronic supplementary material, figure S1, $E^*(t)$ is maximized when it is equal to the marginal energy gain $E'(t)$. In other words, bats remain in the patch for as long as the marginal energy gain $E'(t)$ exceeds the net average gain to date $E^*(t)$.

We used a Runge–Kutta integrator algorithm in R (function ode, method 'lsoda', package deSolve [49]) to solve the above differential equations and evaluate the first time point when $E'(t) < E^*(t)$ as the optimal residence time. We generated model outputs by varying seasonal amplitude k_1 (range: 0 to 0.95), the consumption rate β (range: 0.05 to 1 consumed resource units/t) and the expected time required to travel to a new patch T (range: 0.5 to 72 h). Consumption was always set to start when the resource density was cycling at its equilibrium (i.e. on the limit cycle). To evaluate the effects of variable bat arrival times, we allowed consumption to start when the resource was either at the minimum or maximal resource value of the limit cycle.

(c) Effect of secondary immigration

We then investigated how the residence time changed in response to sudden immigration events associated with floral blooms. We extended equations (2.1)–(2.3) to simulate the arrival of a second bat cohort when food resources $R(t)$ were at their peak:

$$\frac{dR}{dt} = R\left[\nu\left(1 - \frac{R}{K(t)}\right) - \beta_1 - \beta_2\right], \tag{2.6}$$

$$\frac{dE_1}{dt} = \phi\beta_1 R - \mu E_1, \tag{2.7}$$

$$\frac{dE_2}{dt} = \phi\beta_2 R - \mu E_2 \tag{2.8}$$

$$\text{and} \quad K(t) = 1 + k_1 \cos(d2\pi t). \tag{2.9}$$

Here, the subscripts 1 and 2 identify the established and immigrant bat cohorts, respectively. We varied β_2 so that the overall consumption rate was up to 20-fold greater than the consumption rate of the established population β_1, which was introduced at time 0, when the resource density was at its lowest value. For the resident cohort, we set $\beta_1 = 0.05$, $\nu = 1$ and $T = 72$ h, leading to residence times >1.5 years in the absence of immigration (see Results). We then calculated the residence time for both the established bat population and immigrant bats at different seasonality values ($k_1 = 0.25$ or 0.95). In cases of high resource consumption, emigration of arriving bats occurred before the departure of the resident cohort. In these situations, we recalculated the departure time of resident bats by setting $\beta_2 = 0$ when the departure time of the

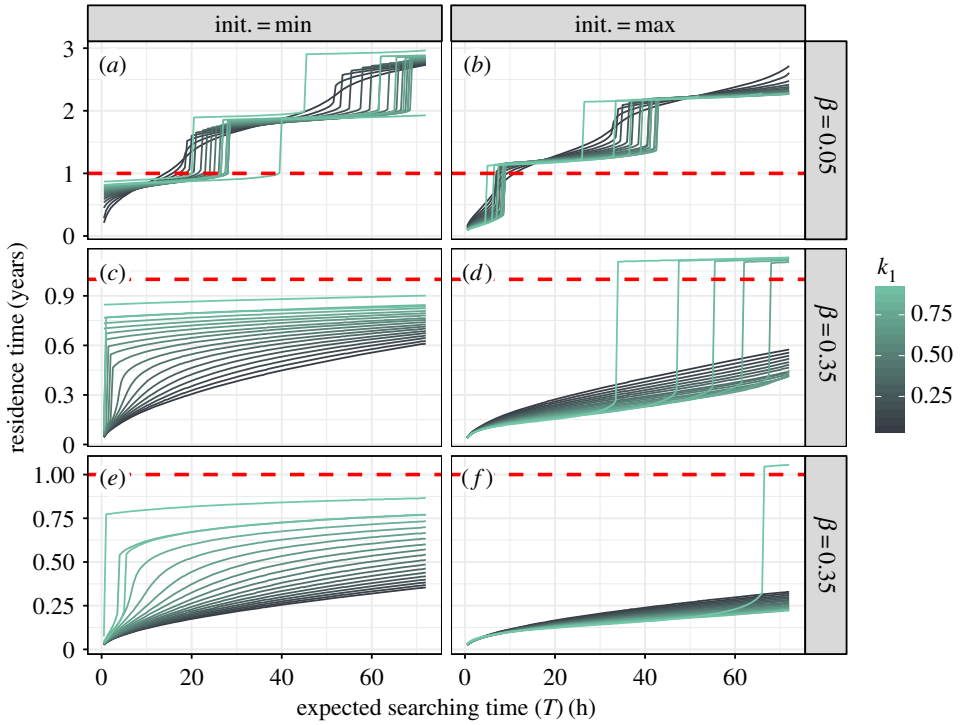

Figure 2. Effects of resource seasonality (k_1), consumption rate (β), initial resource conditions (*Init.*) and expected searching time (T) on the patch residence time. The red dotted line places emphasis on a full year of patch residency. Additional parameter values: the resource generation $\nu = 1$, the metabolic rate $\mu = 0.1$, the resource-to-energy conversion $\phi = 0.5$, and the energetic costs of searching for a new patch $c = 1$.

immigrant cohort occurred (using the 'events' option in the deSolve package in R). This step was also performed to correctly calculate the departure time of immigrant bats following the departure of resident bats.

3. Results

Our first objective was to identify conditions that favour residence in a patch for more than a year (which we refer to as 'overwintering'). In habitats with large seasonal amplitude k_1 and at low consumption rates β, small increases in expected searching time (T) led to bats residing in the patch through complete seasons (figure 2). When comparing the optimal residence time between bats arriving at the peak or the trough of patch productivity (respectively, figure 2*b*,*d*,*f* and figure 2*a*,*c*,*e*) we found a striking pattern: on the one hand, bats that arrived in the low season tended to stay for a few months (but only overwintered if they had a very low consumption rate, (*a*)); on the other hand, bats that arrived at the peak of productivity would either stay for a very short time or overwinter until the next peak.

To better understand these patterns, it is helpful to take a closer look at the dynamics that take place at low consumption rates (i.e. when $\beta = 0.05$, figure 3). When bats arrived at the time of minimum resource abundance (figure 3*a*,*b*), the following generation of resources extended the patch residence time because of high energetic profits. Increasing the expected searching time, which is analogous to making the resource more scarce, also increased the patch residence time because this allowed for higher marginal energetic profits relative to expected gains, even through subsequent periods of resource decay. By contrast, when consumption started at the maximum resource value, the following resource decay was amplified by consumption, leading to low energetic profits and quick departures from the patch. Exceptions to this trend occurred when the searching time was sufficiently high to maintain large marginal energetic profits even under fast resource decay (figure 3*c*). These results suggest that the initial density of the resource (and its subsequent growth or decay) interact with the expected searching time for new patches to determine the residence time in a focal patch.

Next, we asked how resident bats would respond to the arrival of a second bat cohort at peak resource density. We found that the additional resource consumption brought by immigration could result in an earlier departure time of the resident bats. The effect of immigrant bats on the departure time of resident bats, however, depended on the patch's resource seasonality, with an earlier departure more easily achieved in weakly seasonal patches (figure 4 panel *a* versus panel *b*). Overall, these trends depend on the expected searching time T. As T increases, immigration has smaller effects on the residence time of established bats, regardless of the strength of seasonality (results not shown. In figure 4, $T = 20$). Nevertheless, in addition to showing that immigration can affect the departure time of resident bats, our results also show that immigrant bats may also reside for a long period of time in the patch (grey rectangles in figure 4), and that cases of immigration followed by rapid emigration, which occur under high consumption rates, (β_2 in figure 4) can also lower the departure time of resident bats.

4. Discussion

Habitat loss and the availability of food in urban habitats have been hypothesized to cause flying foxes to become resident in urban environments [32]. Consistent with this hypothesis, our results suggest that the ideal conditions for patch residency occur when the cost of travelling to new patches is high and

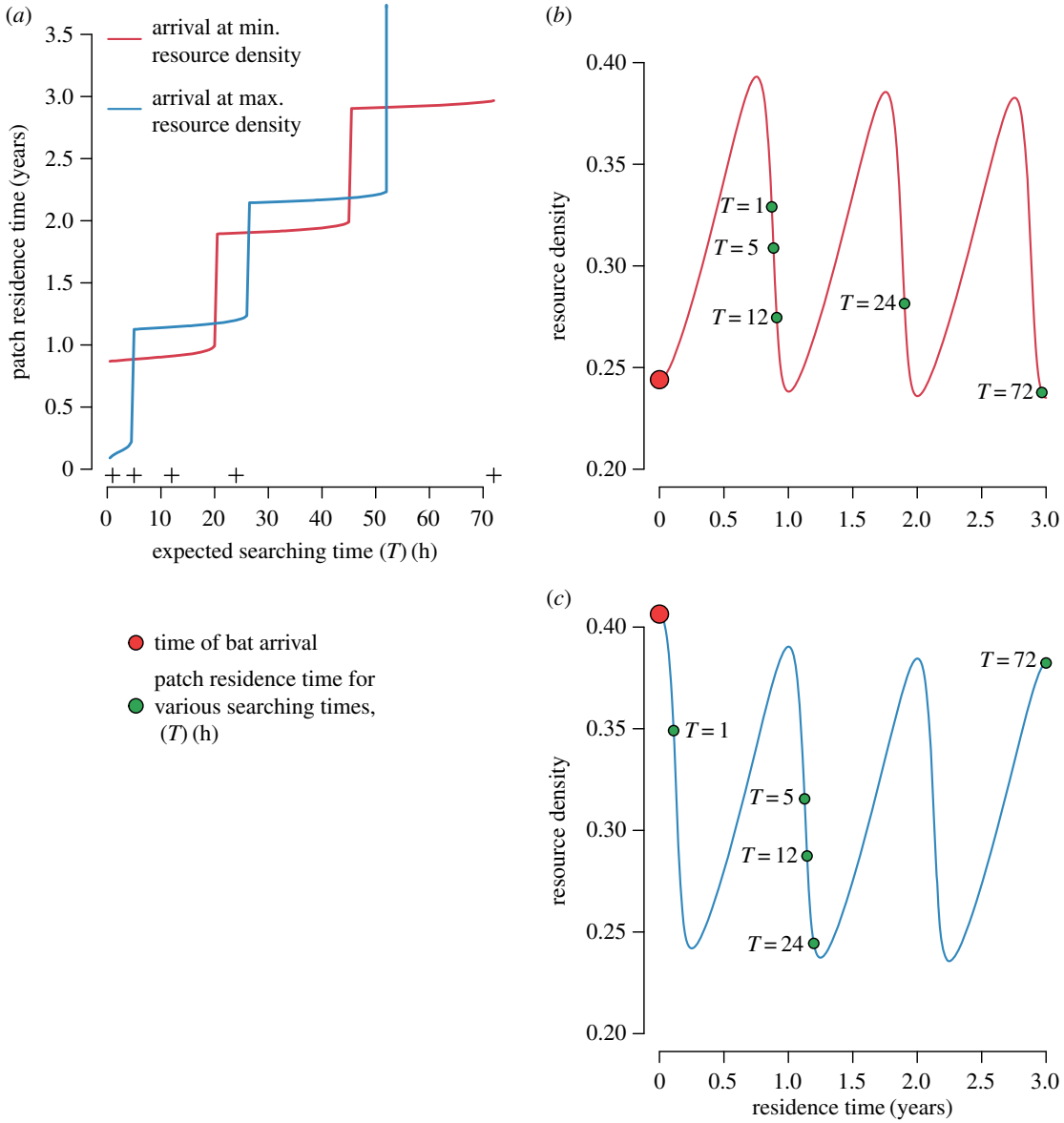

Figure 3. Effect of initial resource density at bat arrival on the patch residence time for two patches with high seasonal resource amplitude $k_1 = 0.95$ and low consumption rate $\beta = 0.05$. (*a*) The patch residence time as a function of the expected searching time (this panel is a subset from the *a*(i)(ii) of figure 2). The cross symbols are the different expected searching times that are then mapped as green dots in panels *b* and *c*. These panels show the resource density as a function of patch residence time. The overlaid green dots show the residence time and corresponding resource density for a given expected search time, *T*. In panel *b* bat arrival occurs at a resource density trough, whereas in panel *c*, bat arrival occurs at peak resource density. Other parameter values are as shown in figure 2.

when the depletion rate of the food source through foraging is low. By contrast, conditions that favour quick departure from a patch are a low cost of travelling and a high rate of resource depletion. Where consumption rates are high, the period of residence is determined by the resource density at the start of consumption, which itself depends on the level of seasonality of the patch's resources. If bats start foraging when resources are at the lowest density, then future resource generation would favour longer patch residence times. By contrast, if bats start foraging at the highest resource value, then rapid resource depletion leads to shorter residence times. Our results show that if bats deplete resources through consumption, patch residence time depends on the timing of bat arrival with respect to the resource density.

In Australia, the flower and fruit production of many native trees is seasonal, with only a few species reliably producing nectar over winter [31,50]. However, flowering phenology is spatially asynchronous, such that the timing of peak flowering differs between sites [32]. The differences in flowering phenology across sites are thus thought to explain the nomadic behaviour of flying foxes, as they track food across the landscape. Our results further suggest that the time that bats reside in a focal patch (i.e. the degree of nomadism) depends on the rate at which resources are consumed within a patch, in addition to the patch's degree of isolation (as measured by the expected time required to find a new patch). However, when consumption is high, the effect of patch isolation on the residence time is small, suggesting that the depletion of food through consumption is the main predictor of nomadic behaviour.

The urbanization of native habitats has changed the composition of flowering tree species, with a mixture of exotic and native foods now probably producing food throughout the year [36,51]. This human effect on the landscape is hypothesized to explained the increased presence of flying foxes in urban habitats [52]. Our results suggest that the residence time does not only depend on constant food availability, but also depends on the initial food density found at bat arrival. For example, a longer residence time in a seasonal food patch

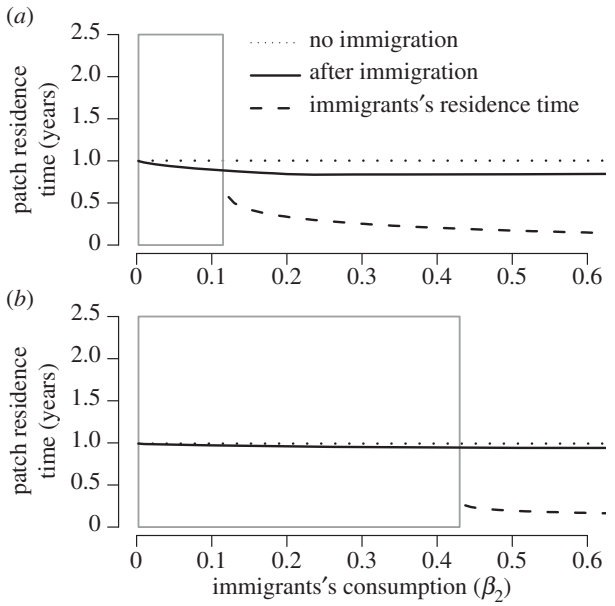

Figure 4. Patch residence time of resident bats after additional resource consumption (β_2) imposed by immigration at peak resource values for weakly seasonal patches ($k_1 = 0.25$ panel *a*) and strongly seasonal patches ($k1 = 0.95$ panel *b*). The grey rectangles delimit β_2 values for which immigrant bats reside for more than 3 years in the patch. Here, the expected searching time, $T = 20$, the consumption of resident bats $\beta_1 = 0.05$, the resource generation $\nu = 1$, the metabolic rate $\mu = 0.1$, the resource-to-energy conversion $\phi = 0.5$, and the energetic costs of searching for a new patch $c = 1$.

compared to a constant food patch is possible if bats arrive at the start of the flowering cycle, because the rapid food generation favours residency. Conversely, if bats arrive to the patch at peak food production, then the following food decay leads to quicker departure times in seasonal food patches compared to constant food patches. Our results thus suggest that consumption rates and food availability are not the only predictors of patch residence time. Under optimal foraging theory, initial food density conditions and the degree patch isolation play an important role in determining the patch residence time.

In contrast to native fruit and nectar which are produced ephemerally, urban areas contain a mixture of exotic and native vegetation that probably produces food throughout the year [36,51]. Thus, the increased presence of flying foxes is often linked to the constant availability of food in urban habitats [52]. Our results suggest that the residence time is influenced by constant food availability, and therefore on a minimal impact of consumption on food density. In habitat patches where food density varies more strongly with season, the residence time also depends on the initial food density at bat arrival. For example, a longer residence time in a seasonal food patch compared to a constant food patch is possible if bats arrive at the start of the flowering cycle, because the rapid food generation favours residency. Conversely, if bats arrive to the patch at peak food production, then the following food decay leads to quicker departure times in seasonal food patches compared to constant food patches. Our results thus suggest that in addition to consumption rates and the degree of patch isolation, the initial food density conditions at bat arrival plays an important role in determining the time that bats will stay in the patch.

Our results also show that new immigration occurring with floral blooms may trigger the departure of resident bats, with immigration reducing the departure time of resident bats to a greater extent in weakly seasonal patches compared to strongly seasonal patches. This effect may be explained by the difference in resource generation and decay between the strongly and weakly seasonal patches. In contrast to the strongly seasonal patch, immigration has a large effect on the resource depletion of weakly seasonal patches. This can then force marginal energetic gains to fall below net average gains made to date, triggering the earlier departure of resident bats. By contrast, in the strongly seasonal patch, the additional effect of immigration may not drastically alter the rate of resource depletion through seasonal decay, or therefore the optimal departure time. This result has the caveat that the expected searching time for new patches can override the effect of immigration, such that isolated patches may experience additional immigration but no emigration. Overall, these results suggest that permanent patch occupation may occur through (1) increased residency through patch isolation, (2) bat turnover in the patch as new immigrant bats trigger the departure of previous bats residing in the patch, rather than because of permanent occupancy of one bat cohort, or (3) immigration at a rate that has little or no effect on resource density (e.g. immigration of only a few bats), but increasing the overall bat population size.

Such contrasting hypotheses about the mechanisms allowing for permanent patch residency have different implications for understanding and managing human–bat interactions, including disease spillover. Although some data exist on patch residence time ([42]; P Eby 2003, unpublished data], more data are needed to test these hypotheses and to quantify the energetic and behavioural mechanisms that create variation in patch residence time. For example, we know that males and females *Pteropus Poliocephalus* have different patch residence times depending on reproductive state (i.e. pregnant and lactating females have higher energetic requirements and change patches more often); that some bats forage over much larger distances [4] than others; and that flight distance is constrained by bat body size and climatic variables such as temperature [4,37,53,54]. This suggests that the energetic benefits of foraging and expected travelling costs are likely to be determined by body size, reproductive state or season. It also suggests that some decisions to migrate or stay put are driven by reproductive considerations and territoriality which may either override or amplify decisions based on energetic demands.

Thus, while processes other than marginal energetic gains may play a role in determining patch residence time, previous studies have argued that movement patterns in Australian pteropodid bats are greatly influenced by the energetic benefits of minimizing commuting distance from roosting to foraging grounds [28,34,37,42,51,55–57]. These arguments are consistent with the theory of optimal foraging and the marginal value theorem used here [44]. Furthermore, our results show that understanding foraging decisions within the context of temporal variation of food resources can provide qualitative approximations of the movement dynamics of pteropodid bats. Further work is, however, required to quantify the parameters influencing these decisions.

Nevertheless, a key issue is that the data suitable for testing our model assumptions are also suitable for testing other models of foraging and movement. One difficulty in developing a mechanistic understanding of patch residence time is that the required data would involve studying animal movement concomitantly with physiology and plant phenology. Models like the ones presented here can guide the design of such studies [58,59], and then be extended to include testable mechanisms of disease

dynamics. For example, foraging models may be used to set time-boundaries under which virus transmission, shedding and spillover can occur in different patches in a metapopulation. Similarly, stochastic model extensions of these foraging decisions could be combined with stochastic epidemic models to evaluate how the movement behaviour of infected individuals affects disease dynamics.

Data accessibility. This article has no additional data.

Authors' contributions. D.J.P., R.K.P. and O.R. developed concepts with advice and assistance from P.E. D.J.P. and O.R. constructed models. D.J.P. performed simulations and summarized results with assistance from O.R. and R.K.P. D.J.P. wrote the initial draft of the paper with editorial input from all authors.

Competing interests. We declare we have no competing interests.

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References

1. Hosseini PR, Dhondt AA, Dobson A. 2004 Seasonality and wildlife disease: how seasonal birth, aggregation and variation in immunity affect the dynamics of Mycoplasma gallisepticum in house finches. *Proc. R. Soc.* **271**, 2569–2577. (doi:10.1098/rspb.2004.2938)
2. Plowright RK, Parrish CR, McCallum H, Hudson PJ, Ko AI, Graham AL, Lloyd-Smith JO. 2017 Pathways to zoonotic spillover. *Nat. Rev. Micro.* **15**, 502–510. (doi:10.1038/nrmicro.2017.45)
3. Dingle H 2014 *Migration: the biology of life on the move*. Oxford, UK: Oxford University Press.
4. Fleming T, Eby P. 2003 *Bat ecology*, chap. Ecology of bat migration (eds TH Kunz, MB Fenton), pp. 156–208. Chicago, IL, USA: University of Chicago Press.
5. Fleming TH, Tuttle MD, Horner MA. 1996 Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran Desert columnar cacti. *Southwest. Nat.* **41**, 257–269.
6. Foo D, Semmens JM, Arnould JP, Dorville N, Hoskins AJ, Abernathy K, Marshall GJ, Hindell MA. 2016 Testing optimal foraging theory models on benthic divers. *Anim. Behav.* **112**, 127–138. (doi:10.1016/j.anbehav.2015.11.028)
7. Seidel DP, Boyce MS. 2015 Patch-use dynamics by a large herbivore. *Mov. Ecol.* **3**, 7. (doi:10.1186/s40462-015-0035-8)
8. Watanabe YY, Ito M, Takahashi A. 2014 Testing optimal foraging theory in a penguin–krill system. *Proc. R. Soc.* **281**, 20132376. (doi:10.1098/rspb.2013.2376)
9. Mitchell WA, Brown JS. 1990 Density-dependent harvest rates by optimal foragers. *Oikos* **57**, 180–190. (doi:10.2307/3565938)
10. Wong BB, Candolin U. 2015 Behavioral responses to changing environments. *Behav. Ecol.* **26**, 665–673. (doi:10.1093/beheco/aru183)
11. Arditi R, Dacorogna B. 1988 Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am. Nat.* **131**, 837–846. (doi:10.1086/284825)
12. Stephens DW, Krebs JR. 1986 *Foraging theory*. Princeton, NJ: Princeton University Press.
13. Kaluza BF, Wallace H, Heard TA, Klein A-M, Leonhardt SD. 2016 Urban gardens promote bee foraging over natural habitats and plantations. *Ecol. Evol.* **6**, 1304–1316. (doi:10.1002/ece3.1941)
14. Møller AP, Tryjanowski P, Díaz M, Kwieciński Z, Indykiewicz P, Mitrus C, Goławski A, Polakowski M. 2015 Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behav. Ecol.* **26**, 861–865. (doi:10.1093/beheco/arv024)
15. Reilly S, Sanderson WT, Christian WJ, Browning SR. 2017 Geographical clusters and predictors of rabies in three southeastern states. *Vector-Borne Zoonotic Dis.* **17**, 432–438. (doi:10.1089/vbz.2016.2061)
16. Plowright RK *et al.* 2015 Ecological dynamics of emerging bat virus spillover. *Proc. R. Soc.* **282**, 20142124. (doi:10.1098/rspb.2014.2124)
17. Altizer S, Dobson A, Hosseini P, Hudson P, Pascual M, Rohani P. 2006 Seasonality and the dynamics of infectious diseases. *Ecol. Lett.* **9**, 467–484. (doi:10.1111/j.1461-0248.2005.00879.x)
18. Hahn MB, Gurley ES, Epstein JH, Islam MS, Patz JA, Daszak P, Luby SP. 2014 The role of landscape composition and configuration on *Pteropus giganteus* roosting ecology and Nipah virus spillover risk in Bangladesh. *Am. J. Trop. Med. Hyg.* **90**, 247–255. (doi:10.4269/ajtmh.13-0256)
19. Sheldon BC, Verhulst S. 1996 Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology and Evolution* **11**, 317–321. (doi:10.1016/0169-5347(96)10039-2)
20. Cressler CE, Graham AL, Day T. 2015 Evolution of hosts paying manifold costs of defence. *Proc. R. Soc.* **282**, 20150065. (doi:10.1098/rspb.2015.0065)
21. Altizer S, Bartel R, Han BA. 2011 Animal migration and infectious disease risk. *Science* **331**, 296–302. (doi:10.1126/science.1194694)
22. Keeling MJ, Rohani P 2008 *Modeling infectious diseases in humans and animals*. Princeton, NJ: Princeton University Press.
23. Hayman DTS, Bowen RA, Cryan PM, McCracken GF, O'Shea TJ, Peel AJ, Gilbert A, Webb CT, Wood JLN. 2013 Ecology of zoonotic infectious diseases in bats: current knowledge and future directions. *Zoonoses Public Health* **60**, 2–21. (doi:10.1111/zph.12000)
24. Calisher CH, Childs JE, Field HE, Holmes KV, Schountz T. 2006 Bats: important reservoir hosts of emerging viruses. *Clin. Microbiol. Rev.* **19**, 531–545. (doi:10.1128/CMR.00017-06)
25. Daszak P, Cunningham AA, Hyatt AD. 2000 Emerging infectious diseases of wildlife–threats to biodiversity and human health. *Science* **287**, 443–449. (doi:10.1126/science.287.5452.443)
26. Martin G, Plowright R, Chen C, Kault D, Selleck P, Skerratt LF. 2015 Hendra virus survival does not explain spillover patterns and implicates relatively direct transmission routes from flying foxes to horses. *J. Gen. Virol.* **96**, 1229–1237. (doi:10.1099/vir.0.000073)
27. Smith C, Skelly C, Kung N, Roberts B, Field H. 2014 Flying-fox species density - a spatial risk factor for Hendra virus infection in horses in eastern Australia. *PLoS ONE* **9**, e99965. (doi:10.1371/journal.pone.0099965)
28. Eby P. 1991 Seasonal movements of grey-headed flying-foxes, *Pteropus poliocephalus* (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. *Wildlife Res.* **18**, 547–559.
29. Spencer H, Palmer C, Parry-Jones K. 1991 Movements of fruit-bats in eastern Australia, determined by using radio-tracking. *Wildlife Res.* **18**, 463–467. (doi:10.1071/WR9910463)
30. Eby P. 1999 Low reproductive output in grey-headed flying-foxes associated with a short period of food scarcity. *Australas. Bat Soc. Newsl.* **14**, 17–20.
31. Law B, Mackowski C, Schoer L, Tweedie T. 2000 Flowering phenology of myrtaceous trees and their relation to climatic, environmental and disturbance variables in northern New South Wales. *Austral Ecol.* **25**, 160–178. (doi:10.1046/j.1442-9993.2000.01009.x)
32. Eby P, Law B. 2008 Ranking the feeding habitat of grey-headed flying foxes for conservation management. Tech. rep., Department of Environment, Heritage, Water and the Arts, Canberra.
33. Field H, Smith C, de Jong C, Melville D, Broos A, Kung N, Thompson J, Dechmann DK. 2016 Landscape utilisation, animal behaviour and Hendra virus risk. *EcoHealth* **13**, 26–38. (doi:10.1007/s10393-015-1066-8)

34. Markus N, Hall L. 2004 Foraging behaviour of the black flying-fox (*Pteropus alecto*) in the urban landscape of Brisbane, Queensland. *Wildlife Res.* **31**, 345–355. (doi:10.1071/WR01117)
35. Parry-Jones K, Augee M. 1991 The diet of flying-foxes in the Sydney and Gosford areas of New South Wales, based on sighting reports 1986–1990. *Aust. Zool.* **27**, 49–54.
36. Hawkins BA. 2014 Birds, fruit and nectar: spatio-temporal patterns of regional bird abundance and food availability in subtropical eastern Australia. PhD thesis, Monash University, Faculty of Science, School of Biological Sciences.
37. Law BS. 1993 Roosting and foraging ecology of the Queensland blossom bat (*Syconycteris australis*) in north-eastern New South Wales: flexibility in response to seasonal variation. *Wildlife Res.* **20**, 419–431. (doi:10.1071/WR9930419)
38. Kung NY, Field HE, McLaughlin A, Edson D, Taylor M. 2015 Flying-foxes in the Australian urban environment—community attitudes and opinions. *One Health* **1**, 24–30. (doi:10.1016/j.onehlt.2015.07.002)
39. Plowright RK, Foley P, Field HE, Dobson AP, Foley JE, Eby P, Daszak P. 2011 Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus* spp.). *Proc. R. Soc.* **278**, 3703–3712. (doi:10.1098/rspb.2011.0522)
40. Andrewartha HG, Birch LC 1986 *The ecological web: more on the distribution and abundance of animals*. Chicago: University of Chicago Press.
41. Bentley B, Elias TS 1983 *The biology of nectaries*. New York, NY: Columbia University Press.
42. Palmer C. 1997 Ecology of the black flying fox, *Pteropus alecto* in the seasonal tropics of the northern territory: resource tracking in a landscape mosaic and role in seed dispersal. PhD thesis, Northern Territory University.
43. Parry-Jones K, Augee M. 1992 Movements of grey-headed flying foxes (*Pteropus poliocephalus*) to and from colony site on the central coast of New South Wales. *Wildlife Res.* **19**, 331–339.
44. Charnov EL. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136. (doi:10.1016/0040-5809(76)90040-X)
45. Fryxell JM, Wilmshurst JF, Sinclair ARE, Haydon DT, Holt RD, Abrams PA. 2005 Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecol. Lett.* **8**, 328–335. (doi:10.1111/j.1461-0248.2005.00727.x)
46. Fryxell JM, Wilmshurst JF, Sinclair AR. 2004 Predictive models of movement by Serengeti grazers. *Ecology* **85**, 2429–2435. (doi:10.1890/04-0147)
47. Bulmer M 1994 *Theoretical evolutionary ecology*. Sunderland, MA: Sinauer Associates.
48. Åström M, Lundberg P, Danell K. 1990 Partial prey consumption by browsers: trees as patches. *J. Anim. Ecol.* **59**, 287–300. (doi:10.2307/5173)
49. Soetaert K, Petzoldt T, Setzer RW. 2010 Solving differential equations in R: Package deSolve. *J. Stat. Softw.* **33**, 1–25. (doi:10.18637/jss.v033.i09)
50. Birt P. 2004 Mutualistic interactions between the nectar-feeding little red flying-fox *Pteropus scapulatus* (Chiroptera: Pteropodidae) and flowering eucalypts (Myrtaceae): habitat utilisation and pollination. PhD thesis, University of Queensland.
51. McDonald-Madden E, Schreiber ESG, Forsyth DM, Choquenot D, Clancy TF. 2005 Factors affecting grey-headed flying-fox (*Pteropus poliocephalus*: Pteropodidae) foraging in the Melbourne metropolitan area, Australia. *Austral Ecol.* **30**, 600–608. (doi:10.1111/j.1442-9993.2005.01492.x)
52. Luskin MS. 2010 Flying foxes prefer to forage in farmland in a tropical dry forest landscape mosaic in fiji. *Biotropica* **42**, 246–250. (doi:10.1111/j.1744-7429.2009.00577.x)
53. Avery MI. 1985 Winter activity of pipistrelle bats. *J. Anim. Ecol.* **54**, 721–738. (doi:10.2307/4374)
54. Westcott DA, Graham DL. 2000 Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* **122**, 249–257. (doi:10.1007/PL00008853)
55. Nelson J. 1965 Movements of Australian flying foxes (Pteropodidae: Megachiroptera). *Aust. J. Zool.* **13**, 53–74. (doi:10.1071/ZO9650053)
56. Palmer C, Woinarski J. 1999 Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the northern territory: resource tracking in a landscape mosaic. *Wildlife Res.* **26**, 823–838. (doi:10.1071/WR97106)
57. Parry-Jones K, Augee M. 2001 Factors affecting the occupation of a colony site in Sydney, New South Wales by the grey-headed flying-fox *Pteropus poliocephalus* (Pteropodidae). *Austral Ecol.* **26**, 47–55. (doi:10.1111/j.1442-9993.2001.01072.pp.x)
58. Dwyer G, Elkinton JS, Buonaccorsi JP. 1997 Host heterogeneity in susceptibility and disease dynamics: tests of a mathematical model. *Am. Nat.* **150**, 685–707. (doi:10.1086/286089)
59. Restif O *et al.* 2012 Model-guided fieldwork: practical guidelines for multidisciplinary research on wildlife ecological and epidemiological dynamics. *Ecol. Lett.* **15**, 1083–1094. (doi:10.1111/j.1461-0248.2012.01836.x)