

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

David J Páez¹, Olivier Restif²

Peggy Eby³, and Raina K. Plowright¹

5 **Affiliations:**

¹Department of Immunology and Microbiology, Montana State University, MT, 59717.
dpaezmc@gmail.com

²Department of Veterinary Medicine, University of Cambridge, United Kingdom, CB3 0ES.
or226@cam.ac.uk

10 ³School of Biological, Earth and Environmental Sciences, University of New South Wales, Australia, 2052. **peby@ozemail.com.au**

RKP: **raina.plowright@montana.edu**

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15 **Corresponding author information:** David Páez, Department of Immunology and Microbiology, Montana State University, MT, 59717. **Ph:** +1 773 993 8875. **dpaezmc@gmail.com**

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20 authors.

Summary

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 non-linear associations between patch residency and loss of native resources that are driven by resource seasonality. 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.

40 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
45 highly mobile and must make decisions about the time spent exploiting a given food patch. Such decisions are likely based on the energetic profitability of the resources and the costs associated with finding a new food patch [3, 4, 5, 6, 7, 8, 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
50 to changes in the distribution, abundance and quality of food resources by adjusting their foraging strategies [10, 11, 12], which may explain 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].

55 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 defense are energetically costly [19, 20]. Similarly, among-hosts dynamics could depend on the foraging decisions made by
60 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, 24, 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
65 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 favor 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
70 [28, 29, 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 [32, 31] is thought to explain the nomadic behavior of flying foxes. However, the four species of flying foxes in Australia differ in their dietary requirements. In urban and peri-urban
75 habitats, generalist species, such as *Pteropus alecto*, exploit a combination of native and exotic food sources [33, 34, 35], which may favor 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
80 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 behavior of flying foxes is affected by a multitude of factors, previous work suggest that flying foxes display optimal foraging behaviors in selecting roosting and foraging sites [37], so that
85 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
90 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
95 quantify the effects of sudden immigration events associated with floral blooms on the patch residence
time of established bats.

Methods

Dynamic model

We built a dynamic model to track resource abundance $R(t)$ in a single patch and the amount of
100 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
105 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
110 time T searching for and traveling 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:

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

$$\frac{dE}{dt} = \phi\beta R - \mu E, \quad (2)$$

$$E(0) = 0, \quad (3)$$

$$K(t) = 1 + k_1 \cos(d2\pi t). \quad (4)$$

115 Decision model

While patch occupancy and migration patterns of flying foxes have been shown to correlate with spatiotemporal variations in food abundance [43, 28], 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 behavior in several animal taxa [45, 46, 47, 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 traveling to the next patch (cT), and “average” as we normalize by the sum of the residence and traveling times:

$$E^*(t) = \frac{E(t) - cT}{T + t}. \quad (5)$$

As shown by [44], and summarized in Supplementary 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 hours). 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.

Effect of secondary immigration

135 We then investigated how the residence time changed in response to sudden immigration events associated with floral blooms. We extended eqns 1-4 to simulate the arrival of a second bat cohort when food resources $R(t)$ were at their peak:

$$\frac{dR}{dt} = R \left[\nu \left(1 - \frac{R}{K(t)} \right) - \beta_1 - \beta_2 \right], \quad (6)$$

$$\frac{dE_1}{dt} = \phi\beta_1 R - \mu E_1, \quad (7)$$

$$\frac{dE_2}{dt} = \phi\beta_2 R - \mu E_2, \quad (8)$$

$$K(t) = 1 + k_1 \cos(d2\pi t). \quad (9)$$

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
 140 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
 145 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 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.

Results

150 Our first objective was to identify conditions that favor 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, right and left-hand panels in
155 Figure 2) 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, top-left panel); 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
160 place at low consumption rates (i.e. when $\beta = 0.05$, Figure 3). When bats arrived at the time of minimum resource abundance (top panel, Figure 3), 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
165 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 (bottom panel Figure 3). These results suggest that the initial density of the resource (and its
170 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
175 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 vs 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
180 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.

Discussion

185 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 traveling to new patches is high and when the depletion rate of the food source through foraging is low. By contrast, conditions that favor quick departure from a patch are a low cost of traveling and a high rate of resource depletion.
190 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 favor 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
195 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 [50, 31]. However, flowering phenology is spatially asynchronous, such that the timing of peak flowering differs between sites [32]. The differences in
200 flowering phenology across sites are thus thought to explain the nomadic behavior 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
205 time is small, suggesting that the depletion of food through consumption is the main predictor of nomadic behavior.

The urbanization of native habitats has changed the composition of flowering tree species, with a mixture of exotic and native foods now likely producing food throughout the year [36, 51]. This human effect on the landscape is hypothesized to explained the increased presence of flying foxes in
210 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 compared to a constant food patch is possible if bats arrive at the start of the flowering cycle, because the rapid food generation favors residency. Conversely, if bats arrive to the patch at peak food production, then the following food decay leads to quicker departure
215 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
220 mixture of exotic and native vegetation that likely 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
225 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 favors 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 exists on patch residence time [42, P. Eby, unpublished data], more data are needed to test these hypotheses and to quantify the energetic and behavioral 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

255 forage over much larger distances [4] than others; and that flight distance is constrained by bat body
size and climatic variables such as temperature [53, 37, 54, 4]. This suggests that the energetic benefits
of foraging and expected traveling 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
260 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 [55, 28, 37, 42, 56, 57, 34, 51]. These arguments are consistent with the theory of
265 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
270 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
275 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 behavior of infected individuals affect
disease dynamics.

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Competing Interests

We have no competing interests.

Figures

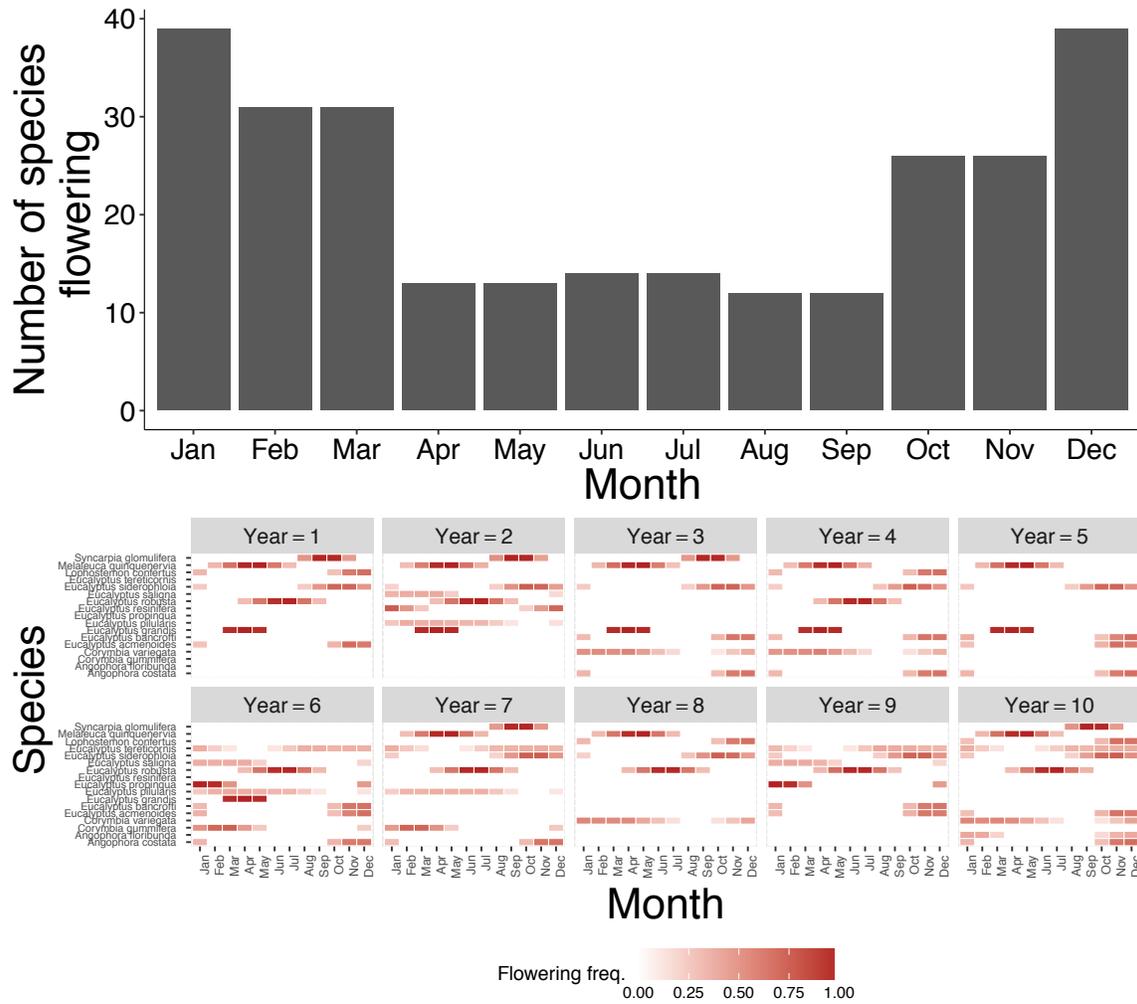


Figure 1: Fewer native tree species flower in winter compared to summer in Australia. Top panel shows the maximum number of species flowering per month out of 56 species known to be nectar food sources for bats in New South Wales, Australia (Data from [32]) The bottom panel shows a simulation of the 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.

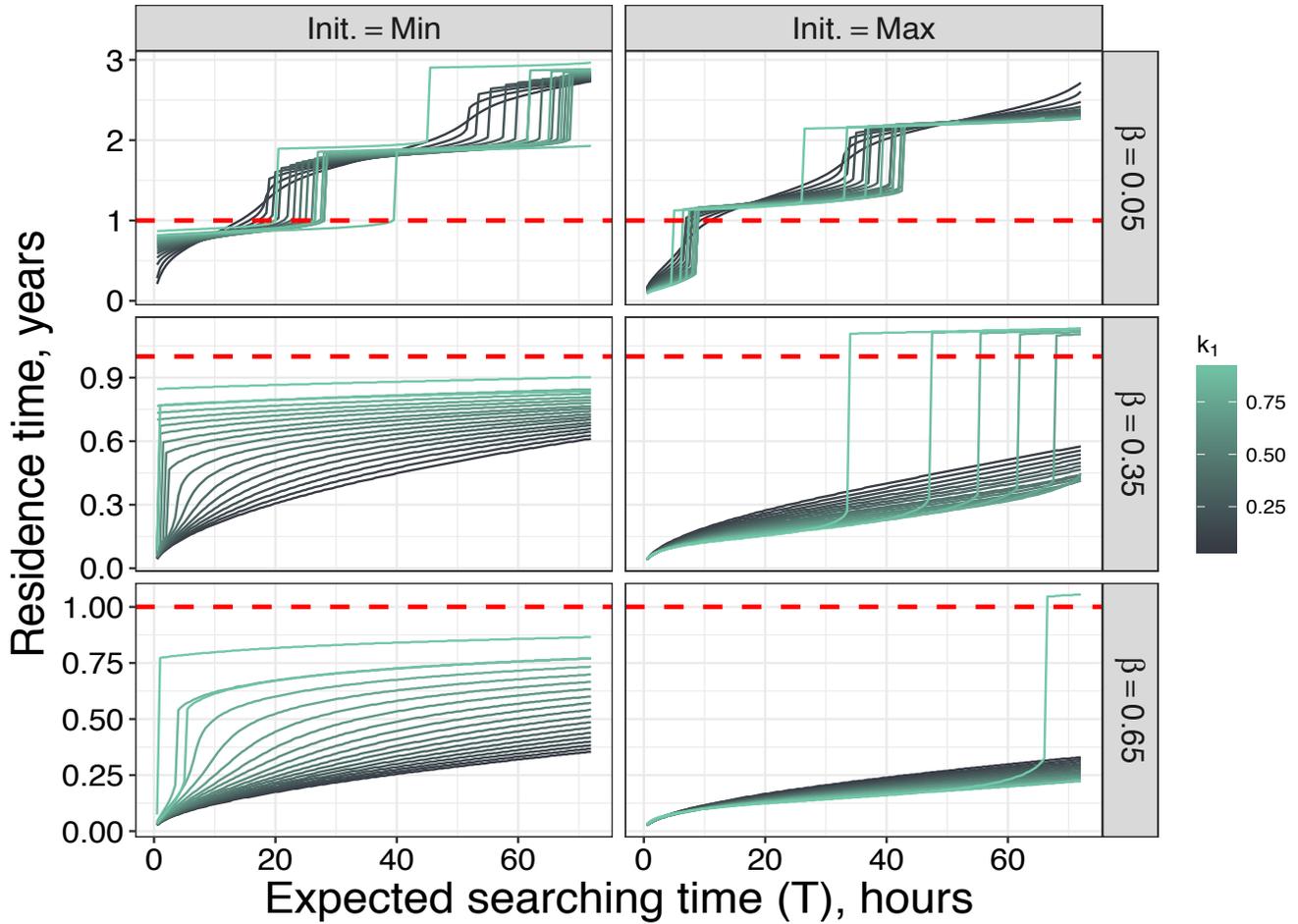
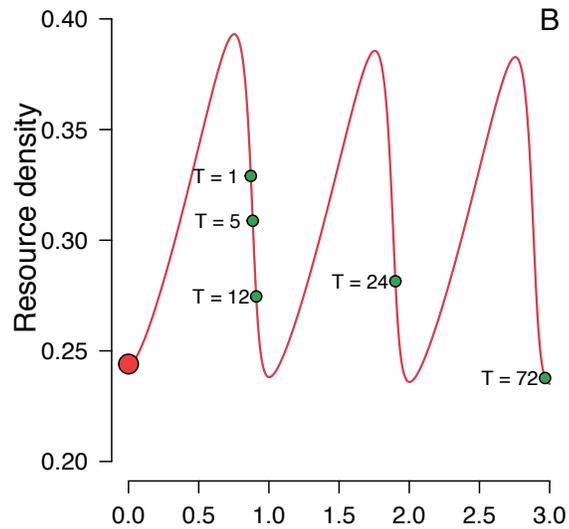
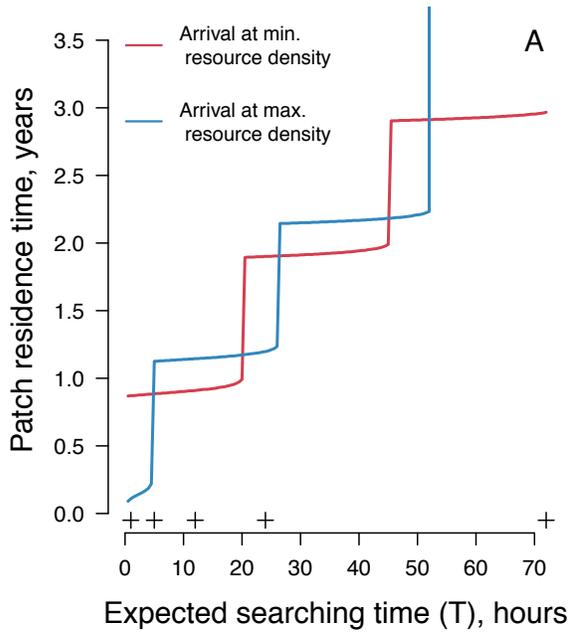


Figure 2: Effects of resource seasonality (k_1), consumption rate (β), Initial resource conditions ($Init.$) and expected searching time (T) on the patch residence time. The red dotted line places emphasis on a full year of patch residency. Additional parameter values: the resource generation $\nu =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



- Time of bat arrival
- Patch residence time for various searching times, T (hours)

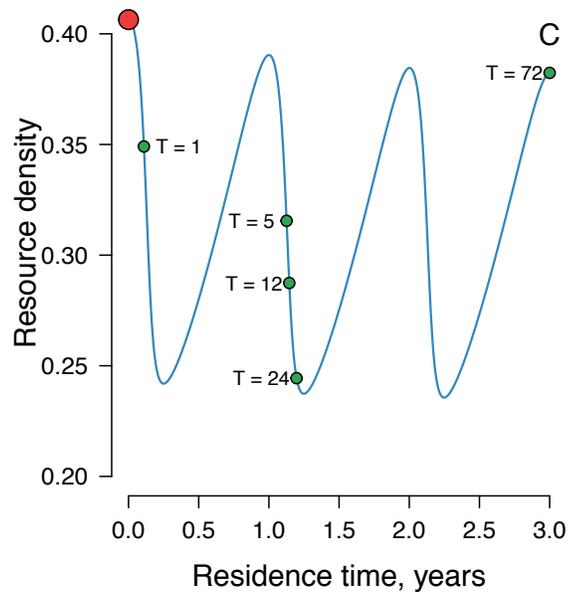


Figure 3: Effect of initial resource density at bat arrival on the patch residence time for two patches with high seasonal resource amplitude $k_1 = 0.95$ and low consumption rate $\beta = 0.05$. Panel A shows the patch residence time as a function of the expected searching time (this panel is a subset from the top row panels 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.

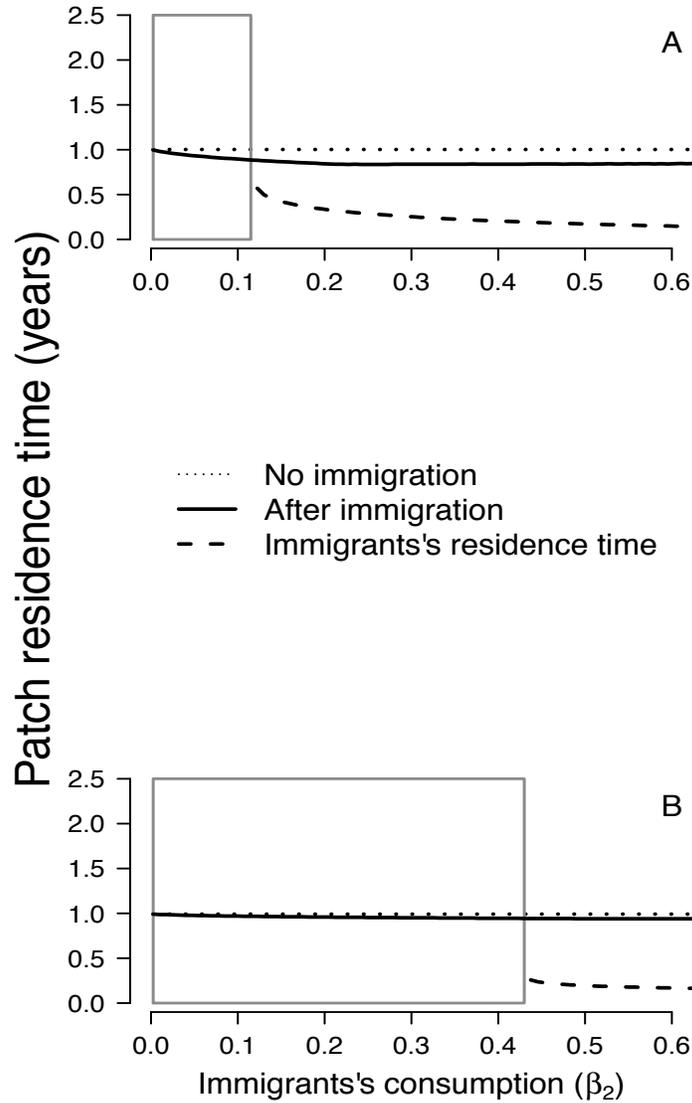


Figure 4: Patch residence time of resident bats after additional resource consumption (β_2) imposed by immigration at peak resource values for weakly seasonal patches ($k_1 = 0.25$ panel A) and strongly seasonal patches ($k_1 = 0.95$ panel B). The grey rectangles delimit β_2 values for which immigrant 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 $c = 1$.

290 References

- [1] Hosseini PR, Dhondt AA, Dobson A. Seasonality and wildlife disease: how seasonal birth, aggregation and variation in immunity affect the dynamics of *Mycoplasma gallisepticum* in house finches. *Proceedings of the Royal Society of London B: Biological Sciences*. 2004;271:2569–2577.
- 295 [2] Plowright RK, Parrish CR, McCallum H, Hudson PJ, Ko AI, Graham AL, et al. Pathways to zoonotic spillover. *Nat Rev Micro*. 2017;15(8):502–510.
- [3] Dingle H. *Migration: the biology of life on the move*. Oxford University Press, USA; 2014.
- [4] Fleming TH, Eby P. Ecology of bat migration. In: Kunz TH, Fenton MB, editors. *Bat Ecology*. University of Chicago Press.; 2003.. p. 156–208.
- 300 [5] Fleming TH, Tuttle MD, Horner MA. Pollination Biology and the Relative Importance of Nocturnal and Diurnal Pollinators in Three Species of Sonoran Desert Columnar Cacti. *The Southwestern Naturalist*. 1996;41:257–269.
- [6] Foo D, Semmens JM, Arnould JPY, Dorville N, Hoskins AJ, Abernathy K, et al. Testing optimal foraging theory models on benthic divers. *Animal Behaviour*. 2016;112:127 – 138.
- 305 [7] Seidel DP, Boyce MS. Patch-use dynamics by a large herbivore. *Movement Ecology*. 2015;3:7.
- [8] Watanabe YY, Ito M, Takahashi A. Testing optimal foraging theory in a penguin–krill system. *Proceedings of the Royal Society of London B: Biological Sciences*. 2014;281(1779).
- [9] Mitchell WA, Brown JS. Density-Dependent Harvest Rates by Optimal Foragers. *Oikos*. 1990;57:180–190.
- 310 [10] Wong BBM, Candolin U. Behavioral responses to changing environments. *Behavioral Ecology*. 2015;26(3):665.

- [11] Arditi R, Dacorogna B. Optimal Foraging on Arbitrary Food Distributions and the Definition of Habitat Patches. *The American Naturalist*. 1988;131(6):837–846.
- [12] Stephens DW, Krebs JR. *Foraging theory*. Princeton University Press; 1986.
- 315 [13] Kaluza BF, Wallace H, Heard TA, Klein AM, Leonhardt SD. Urban gardens promote bee foraging over natural habitats and plantations. *Ecology and Evolution*. 2016;6(5):1304–1316.
- [14] Møller AP, Tryjanowski P, Díaz M, Kwieciński Z, Indykiewicz P, Mitrus C, et al. Urban habitats and feeders both contribute to flight initiation distance reduction in birds. *Behavioral Ecology*. 2015;26(3):861–865.
- 320 [15] Reilly S, Sanderson WT, Christian WJ, Browning SR. Geographical Clusters and Predictors of Rabies in Three Southeastern States. *Vector-Borne and Zoonotic Diseases*. 2017;17(6):432–438.
- [16] Plowright RK, Eby P, Hudson PJ, Smith IL, Westcott D, Bryden WL, et al. Ecological dynamics of emerging bat virus spillover. *Proceedings of the Royal Society of London B: Biological Sciences*. 2015;282(1798).
- 325 [17] Altizer S, Dobson A, Hosseini P, Hudson P, Pascual M, Rohani P. Seasonality and the dynamics of infectious diseases. *Ecology letters*. 2006;9(4):467–484.
- [18] Hahn MB, Gurley ES, Epstein JH, Islam MS, Patz JA, Daszak P, et al. The role of landscape composition and configuration on *Pteropus giganteus* roosting ecology and Nipah virus spillover risk in Bangladesh. *The American journal of tropical medicine and hygiene*. 2014;90(2):247–255.
- 330 [19] Sheldon BC, Verhulst S. Ecological immunology: costly parasite defences and trade-offs in evolutionary ecology. *Trends in Ecology & Evolution*. 1996;11(8):317 – 321.
- [20] Cressler CE, Graham AL, Day T. Evolution of hosts paying manifold costs of defence. *Proceedings of the Royal Society of London B: Biological Sciences*. 2015;282:20150065.
- [21] Altizer S, Bartel R, Han BA. Animal migration and infectious disease risk. *science*.
335 2011;331:296–302.

- [22] Keeling MJ, Rohani P. Modeling infectious diseases in humans and animals. Princeton University Press; 2008.
- [23] Hayman DTS, Bowen RA, Cryan PM, McCracken GF, O'Shea TJ, Peel AJ, et al. Ecology of Zoonotic Infectious Diseases in Bats: Current Knowledge and Future Directions. *Zoonoses and Public Health*. 2013;60(1):2–21.
- 340 [24] Calisher CH, Childs JE, Field HE, Holmes KV, Schountz T. Bats: important reservoir hosts of emerging viruses. *Clinical microbiology reviews*. 2006;19(3):531–545.
- [25] Daszak P, Cunningham AA, Hyatt AD. Emerging infectious diseases of wildlife—threats to biodiversity and human health. *science*. 2000;287(5452):443–449.
- 345 [26] Martin G, Plowright R, Chen C, Kault D, Selleck P, Skerratt LF. Hendra virus survival does not explain spillover patterns and implicates relatively direct transmission routes from flying foxes to horses. *Journal of General Virology*. 2015;96(6):1229–1237.
- [27] Smith C, Skelly C, Kung N, Roberts B, Field H. Flying-Fox Species Density - A Spatial Risk Factor for Hendra Virus Infection in Horses in Eastern Australia. *PLoS ONE*. 2014 06;9(6):1–7.
- 350 [28] Eby P. Seasonal movements of grey-headed flying-foxes, *Pteropus poliocephalus* (Chiroptera: Pteropodidae), from two maternity camps in northern New South Wales. *Wildlife Research*. 1991;18:547–559.
- [29] Spencer H, Palmer C, Parry-Jones K. Movements of fruit-bats in eastern Australia, determined by using radio-tracking. *Wildlife Research*. 1991;18(4):463–467.
- 355 [30] Eby P. Low reproductive output in Grey-headed Flying-foxes associated with a short period of food scarcity. *Australasian Bat Society Newsletter*. 1999;14:17–20.
- [31] Law B, Mackowski C, Schoer L, Tweedie T. Flowering phenology of myrtaceous trees and their relation to climatic, environmental and disturbance variables in northern New South Wales. *Austral Ecology*. 2000;25(2):160–178.

- 360 [32] Eby P, Law B. Ranking the feeding habitat of grey-headed flying foxes for conservation
management. Canberra: Department of Environment, Heritage, Water and the Arts; 2008.
- [33] Field H, Smith C, de Jong C, Melville D, Broos A, Kung N, et al. Landscape utilisation, animal
behaviour and Hendra virus risk. *EcoHealth*. 2016;13:26–38.
- [34] Markus N, Hall L. Foraging behaviour of the black flying-fox (*Pteropus alecto*) in the urban
365 landscape of Brisbane, Queensland. *Wildlife Research*. 2004;31(3):345–355.
- [35] Parry-Jones K, Augee M. The diet of Flying-foxes in the Sydney and Gosford areas of New South
Wales, based on sighting reports 1986-1990. *Australian Zoologist*. 1991;27(3-4):49–54.
- [36] Hawkins BA. Birds, fruit and nectar: spatio-temporal patterns of regional bird abundance and
food availability in subtropical eastern Australia. Monash University. Faculty of Science. School
370 of Biological Sciences; 2014.
- [37] Law BS. Roosting and foraging ecology of the Queensland blossom bat (*Syconycteris australis*) in
north-eastern New South Wales: flexibility in response to seasonal variation. *Wildlife Research*.
1993;20(4):419–431.
- [38] Kung NY, Field HE, McLaughlin A, Edson D, Taylor M. Flying-foxes in the Australian urban
375 environmentâ€”community attitudes and opinions. *One Health*. 2015;1:24 – 30.
- [39] Plowright RK, Foley P, Field HE, Dobson AP, Foley JE, Eby P, et al. Urban habituation, ecological
connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes
(*Pteropus* spp.). *Proceedings of the Royal Society of London B: Biological Sciences*.
2011;278:3703–3712.
- 380 [40] Andrewartha HG, Birch LC. The ecological web: more on the distribution and abundance of
animals. University of Chicago Press; 1986.
- [41] Bentley B, Elias TS. The biology of nectaries. Columbia University Press; 1983.

- [42] Palmer C. 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. Northern Territory University; 1997.
- [43] Parry-Jones K, Augee M. Movements of grey-headed flying foxes (*Pteropus poliocephalus*) to and from colony site on the central coast of New South Wales. *Wildlife Research*. 1992;19(3):331–339.
- [44] Charnov EL. Optimal foraging, the marginal value theorem. *Theoretical population biology*. 1976;9:129–136.
- 390 [45] Fryxell JM, Wilmshurst JF, Sinclair ARE, Haydon DT, Holt RD, Abrams PA. Landscape scale, heterogeneity, and the viability of Serengeti grazers. *Ecology Letters*. 2005;8:328–335.
- [46] Fryxell JM, Wilmshurst JF, Sinclair AR. Predictive models of movement by Serengeti grazers. *Ecology*. 2004;85:2429–2435.
- [47] Bulmer M. *Theoretical evolutionary ecology*. Sinauer Associates Sunderland, MA; 1994.
- 395 [48] Åström M, Lundberg P, Danell K. Partial Prey Consumption by Browsers: Trees as Patches. *Journal of Animal Ecology*. 1990;59(1):287–300.
- [49] Soetaert K, Petzoldt T, Setzer RW. Solving Differential Equations in R: Package deSolve. *Journal of Statistical Software*. 2010;33(9):1–25.
- [50] Birt P. Mutualistic interactions between the nectar-feeding little red flying-fox *Pteropus scapulatus* (Chiroptera: Pteropodidae) and flowering eucalypts (Myrtaceae): habitat utilisation and pollination. University of Queensland; 2004.
- 400 [51] McDonald-Madden E, Schreiber ESG, Forsyth DM, Choquenot D, Clancy TF. Factors affecting Grey-headed Flying-fox (*Pteropus poliocephalus*: Pteropodidae) foraging in the Melbourne metropolitan area, Australia. *Austral Ecology*. 2005;30(5):600–608.
- 405 [52] Luskin MS. Flying foxes prefer to forage in farmland in a tropical dry forest landscape mosaic in Fiji. *Biotropica*. 2010;42(2):246–250.

- [53] Avery MI. Winter Activity of Pipistrelle Bats. *Journal of Animal Ecology*. 1985;54(3):721–738.
- [54] Westcott DA, Graham DL. Patterns of Movement and Seed Dispersal of a Tropical Frugivore. *Oecologia*. 2000;122(2):249–257.
- 410 [55] Nelson J. Movements of Australian flying foxes (Pteropodidae: Megachiroptera). *Australian Journal of Zoology*. 1965;13(1):53–74.
- [56] Palmer C, Woinarski J. Seasonal roosts and foraging movements of the black flying fox (*Pteropus alecto*) in the Northern Territory: resource tracking in a landscape mosaic. *Wildlife Research*. 1999;26:823–838.
- 415 [57] Parry-Jones K, Augee M. Factors affecting the occupation of a colony site in Sydney, New South Wales by the Grey-headed Flying-fox *Pteropus poliocephalus* (Pteropodidae). *Austral Ecology*. 2001;26:47–55.
- [58] Dwyer G, Elkinton JS, Buonaccorsi JP. Host heterogeneity in susceptibility and disease dynamics: tests of a mathematical model. *The American Naturalist*. 1997;150:685–707.
- 420 [59] Restif O, Hayman DTS, Pulliam JRC, Plowright RK, George DB, Luis AD, et al. Model-guided fieldwork: practical guidelines for multidisciplinary research on wildlife ecological and epidemiological dynamics. *Ecology Letters*. 2012;15:1083–1094.

Supplementary Material

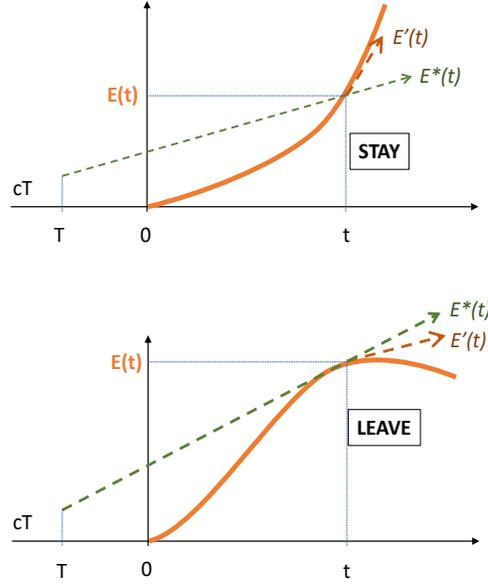


Figure S1: Patch departure times based on their marginal value theorem. The average energy gain acquired by exploiting a patch for t units of time, followed by travel time T to a new patch at the expense of cT energy units is defined as: $E^*(t) = \frac{E(t) - cT}{t + T}$. The marginal gain of energy at time t is the derivative $E'(t)$. If the bat stays in the patch for an extra ∂t time units, it can expect to acquire $E'(t)\partial t$ energy units, so that the new average gain will be:

$$E^*(t + \partial t) = \frac{E(t) + E'(t)\partial t - cT}{t + \partial t + T}$$

$$= \frac{E^*(t)(t + T)}{t + \partial t + T} + \frac{E'(t)\partial t}{t + \partial t + T}$$

The decision to stay (top panel) or leave (bottom) is based on maximizing the average gain in this patch. The bat will leave at time t if the average gain E^* is expected to decrease between t and $t + \partial t$:

$$E^*(t + \partial t) - E^*(t) < 0.$$

We can then re-write the change as:

$$E^*(t + \partial t) - E^*(t) = \frac{E^*(t) - E'(t)}{\partial t / (t + \partial t + T)}.$$

In other words, the bats should stay for as long as the marginal gain $E'(t)$ is higher the average gain so far $E^*(t)$.