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Animal behaviour

Pairing automated mark–recapture and social network models to explore the effects of landscape configuration on hummingbird foraging patterns

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Landscape changes can alter pollinator movement and foraging patterns which can in turn influence the demographic processes of plant populations. We leveraged social network models and four fixed arrays of five hummingbird feeders equipped with radio frequency identification (RFID) data loggers to study rufous hummingbird (*Selasphorus rufus*) foraging patterns in a heterogeneous landscape. Using a space-for-time approach, we asked whether forest encroachment on alpine meadows could restrict hummingbird foraging movements and impede resource discovery. We fit social network models to data on 2221 movements between feeders made by 29 hummingbirds. Movements were made primarily by females, likely due to male territoriality and early migration dates. Distance was the driving factor in determining the rate of movements among feeders. The posterior mean effects of forest landscape variables (local canopy cover and intervening forest cover) were negative, but with considerable uncertainty. Finally, we found strong reciprocity in hummingbird movements, indicative of frequent out and back movements between resources. Together, these findings suggest that reciprocal movements by female hummingbirds could help maintain bidirectional gene flow among nearby subpopulations of ornithophilous plants; however, if the distance among meadows increases with further forest encroachment, this may limit foraging among progressively isolated meadows.

1. Introduction

In the Cascade Mountains of the western United States, rapid forest encroachment is shrinking and fragmenting alpine meadows that support diverse plant and pollinator communities [1]. Woody encroachment is known to have adverse impacts on herbaceous plant communities through changes to environmental conditions, such as light and soil characteristics [2–5]; however, the decline of meadow communities could be expedited if increased tree and shrub cover limits pollinator movement through the landscape. Limited pollinator movement could result in reduced seed set and recruitment in subpopulations of outcrossing plants [6,7].

Because of the long timescale over which forest encroachment occurs, we used a 'space-for-time' approach in which we exchanged differences in landscape context at a fixed location over time for current differences across locations in space to infer how future changes in the landscape may influence functional connectivity.
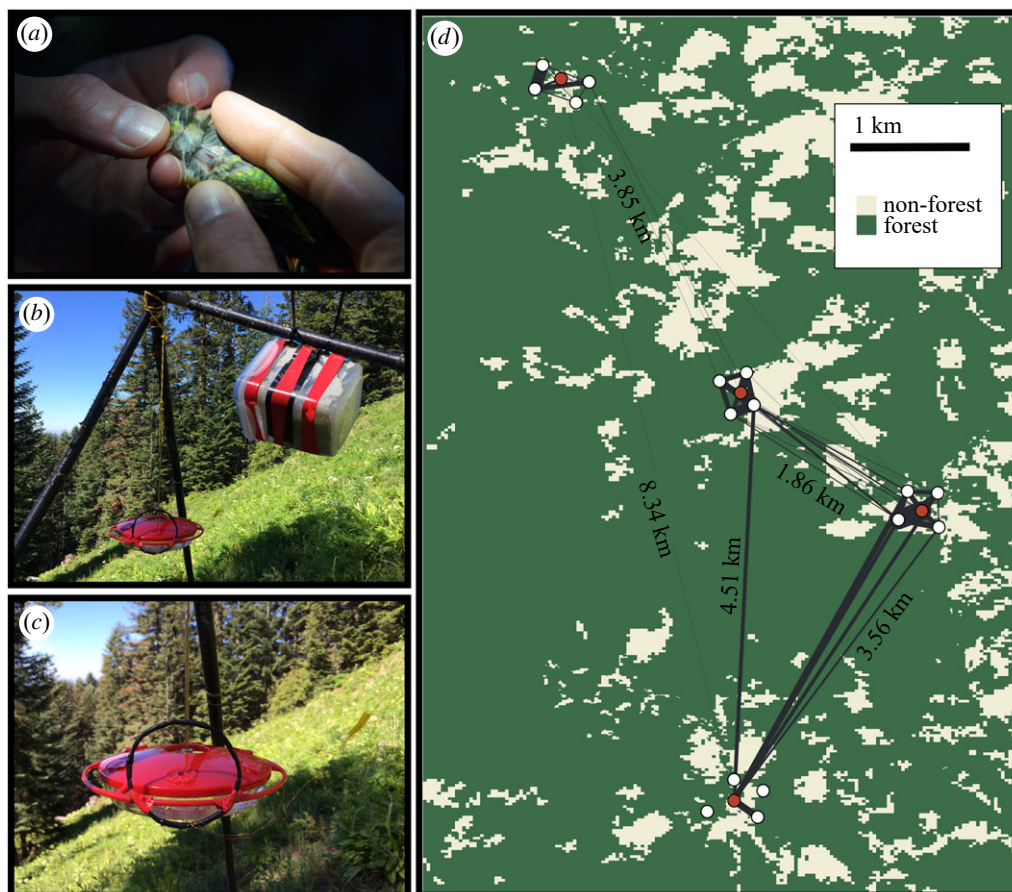
Figure 1. (*a*) Recaptured rufous-tailed hummingbird (*Amazilia tzacatl*) with a PIT tag. (*b*) RFID reader–feeder set-up with datalogger. (*c*) A copper coil (antenna) wrapped in electrical tape and attached to the hummingbird feeder triggers records from passing PIT tags. All but one port in the feeder were covered. (*d*) Arrays of RFID-equipped feeders in the mixed-cover landscape. Capture locations are coloured red. Lines connecting the readers are scaled to reflect the total number of movements detected among feeders.

We collected data on movement rates by hummingbirds implanted with passive integrated transponders (PIT tags [8]) among feeders placed throughout a mixed-cover landscape. We then fit 'sender–receiver' models developed for social network data [9–11] to assess the functional connectivity of different locations across the landscape [12]. These methods offer multiple benefits. First, our methods employ passive mark–recapture techniques which may yield large volumes of data with reduced labour cost [13]. Second, sender–receiver models allow us to estimate the effects of landscape features on the connectivity of fixed locations in a generalized regression framework and allow insight into movement patterns such as the reciprocity of movements which may elucidate source–sink dynamics (emigration out of high-density areas with minimal immigration) and directional gene flow.

We sought to test two hypotheses of how forest encroachment could reduce the connectivity of meadow plant populations by limiting foraging movements of rufous hummingbirds (*Selasphorus rufus*), common avian pollinators in the western United States. First, woody vegetation could act as a barrier to foraging movements if hummingbirds establish territories in open areas and limit foraging search patterns to open habitat with minimal exploration into forested areas (we refer to this hypothesis as the *barrier hypothesis*). If true, we predicted that movement rates should be reduced between feeders placed in meadows separated by closed canopy forest and also to feeders placed inside the forest. This barrier to movement could reduce effective population sizes by reducing

visitation to plants that get overgrown by forest species as well as pollen flow among subpopulations.

Second, hummingbirds could avoid flying through closed canopy forest, but fly over the canopy to forage in disconnected meadows [14]. This behaviour could result in reduced capacity for birds to detect plants within forests but would not limit movements among meadows (*resource discovery hypothesis*). In this scenario, we predicted reduced movement rates to feeders placed inside the forest but not those placed in open habitat, regardless of the intervening landscape. Thus, hummingbirds could help maintain connectivity among subpopulations of ornithophilous plants, but the effective population size may still decline as some plants are overgrown by woody vegetation and visited less by pollinators.

2. Methods

We established four study sites in meadow complexes (clusters of meadows) located on summits that span the north–south extent of the H.J. Andrews Experimental Forest (AND), Oregon, USA (44.212° N, 122.256° E). The sites were selected such that we could establish arrays of five hummingbird feeders with one feeder in a central meadow and four satellite feeders *ca* 250 m from the centre (figure 1*d*). The satellite feeders were placed with at least one under closed canopy coniferous forest ($n = 5$), one in a meadow separated from the centre feeder by closed canopy ($n = 4$) and one in a meadow connected to the centre feeder by open habitat ($n = 7$). We established hummingbird

Table 1. Posterior means and percentiles for the regression parameters of interest. β_{distance} is the effect of the distance between two feeders on the log-movement rate between them, β_{forest} is the effect of the proportion of forested area in the 50 m belt transect between two feeders and β_{cover} is the effect of local canopy cover (feeders inside the forest or not) on log-movement rate.

parameter	mean	2.5%	25%	50%	75%	97.5%
β_0 (intercept)	−2.87	−4.58	−3.52	−2.91	−2.25	−0.97
β_{distance}	−1.46	−1.72	−1.54	−1.46	−1.37	−1.21
β_{forest}	−0.60	−1.92	−1.07	−0.59	−0.14	0.69
β_{cover}	−1.18	−3.08	−1.81	−1.18	−0.55	0.67

feeders filled with 20% sugar water solution at the centre meadow in each meadow complex (figure 1) two weeks before trapping hummingbirds. Following the two-week habituation period, we placed Hall traps [15] around the centre feeders and monitored them for a period of 5 h (05.00–10.00). We collected standard measurements on each trapped individual and banded each with a unique metal leg band. The final processing step was to implant the PIT tag under the loose skin between the shoulders (figure 1a and electronic supplementary material, figures S1–S14). The full details of our procedure can be found in the electronic supplementary material.

Over the course of four summers (mid-June through July 2014–2017), we captured and implanted 163 rufous hummingbirds with PIT tags. To automatically record the locations of individuals following the initial capture, we established the four arrays of hummingbird feeders as described above, equipped with radio-frequency identification (RFID) data loggers (figure 1b,c). When a hummingbird visited a feeder, the PIT tag passed through a copper coil placed around the sole access point (figure 1c), logging the time, date and individual identification code (further details on adjusting the methods in [8] for this system can be found in the electronic supplementary material). Feeders were maintained for 1.5–12 weeks per year for up to 4 years (the southernmost array was established in 2015 and the northernmost array was established in 2016; figure 1d).

We extracted movement information from the relocation data by tallying occasions on which an individual was recorded at feeder i at time t and again at feeder j, $j \neq i$, at time t', $t' > t$, within the same day. We limited our focus to movement that occurred within the same day to gain insight into hummingbird movements that may be relevant to pollination. Additionally, we summed the movements over the summer to get multiple measurements of movement between two feeders (one per year) that can more reasonably be treated as independent given the regression parameters. While we lose information on inter-individual differences in foraging behaviours by summing movements over the year, our objective was to model functional connectivity informed by hummingbird movements. Whether a given number of movements is made by many birds each making few movements or by few birds making many movements is not important in this endeavour.

Briefly (but see the electronic supplementary material for full details), we treated each feeder as a node in a graph and modelled the edge weight (connectivity between two nodes) of directed edges (i.e. $\lambda_{ij} \neq \lambda_{ji}$) in the graph. We denote λ_{ij} as the weight of the edge connecting node i to j and assume that the number of movements between two feeders in a given year, $y_{ijk} \in \mathbb{N}$, where $k = 1,2,\ldots,K$ indexes the year, was a draw from a Poisson distribution with rate parameter λ_{ijk}. Thus, in year k, when R_k feeders were maintained on the landscape, there were $n_k = R_k(R_k - 1)$ possible movements, yielding $N = \sum_{k=1}^{K} n_k$ total observations.

Within this framework, we fit a 'sender–receiver' regression model [9–11] using the R package 'rstan' [16,17] that accounts for dependencies among movements that share a common origin,

those that share a common destination, and dependence within a dyad (i.e. frequency of movements $i \rightarrow j$ and $j \rightarrow i$). Our covariates of interest included the effect of geographic distance between feeders i and j (β_{distance}), the amount of intervening forest in a 50-m belt transect between i and j (β_{forest}), and the average of two indicator variables (β_{cover}), one indicating whether feeder i was in the forest and one indicating whether feeder j was in the forest ($x_{ij,\text{cover}} \in \{0,0.5,1\}$). Strong negative effects of both placing a feeder under the canopy and the amount of intervening forest would support the barrier hypothesis, while a negative effect of placing a feeder under the canopy combined with a negligible or positive effect of intervening forest would support the resource discovery hypothesis. For each year, we included offsets for the number of weeks a given pair of feeders was available to the birds and the cumulative number of birds that were implanted with PIT tags. Ninety-five percent credible intervals for parameters of interest are presented below in square brackets and in table 1.

3. Results

Over the course of four summers (June–August), the four arrays of hummingbird feeders equipped with passive data loggers recorded 20 877 separate relocations (reads spaced by greater than 30 s) of 63 rufous hummingbirds (13 males, 40 females and 10 of unknown sex), 51 of which were recorded on multiple days (12 males, 33 females and six of unknown sex) and eight over multiple years (one male and seven females). From these data, we extracted information on 2221 movements between feeders made by 29 hummingbirds (two males and 27 females). Data on the birds that did not move among feeders can be found in the electronic supplementary material. Our final dataset included data on the number of times each of the n_k network connections was made in year k ($N = 1060$ total edge measurements).

The majority of movements were among feeders within an array. Only 362 of the recorded movements (made by eight birds, one male and seven females) were between two feeder arrays (figure 1d), indicating that home ranges did not often span an area that covered multiple meadow complexes. The fitted model predicts that the probability of at least one movement between two feeders per bird per week approaches zero when feeders are greater than 2 km apart (table 1 and figure 2).

The posterior means of both forest landscape coefficients were negative, but with relatively high uncertainty (table 1). The expected effect of intervening forest on the log-movement rate is $\hat{\beta}_{\text{forest}} = -0.60 \, [-1.92, 0.69]$ and the expected effect of local canopy cover (placing feeders inside the forest) is $\hat{\beta}_{\text{cover}} = -1.18 \, [-3.08, 0.67]$. Finally, we found high reciprocity in the hummingbird movements (correlation of dyad effects was $\hat{\rho} = 0.97 \, [0.92, 0.99]$), indicating movement
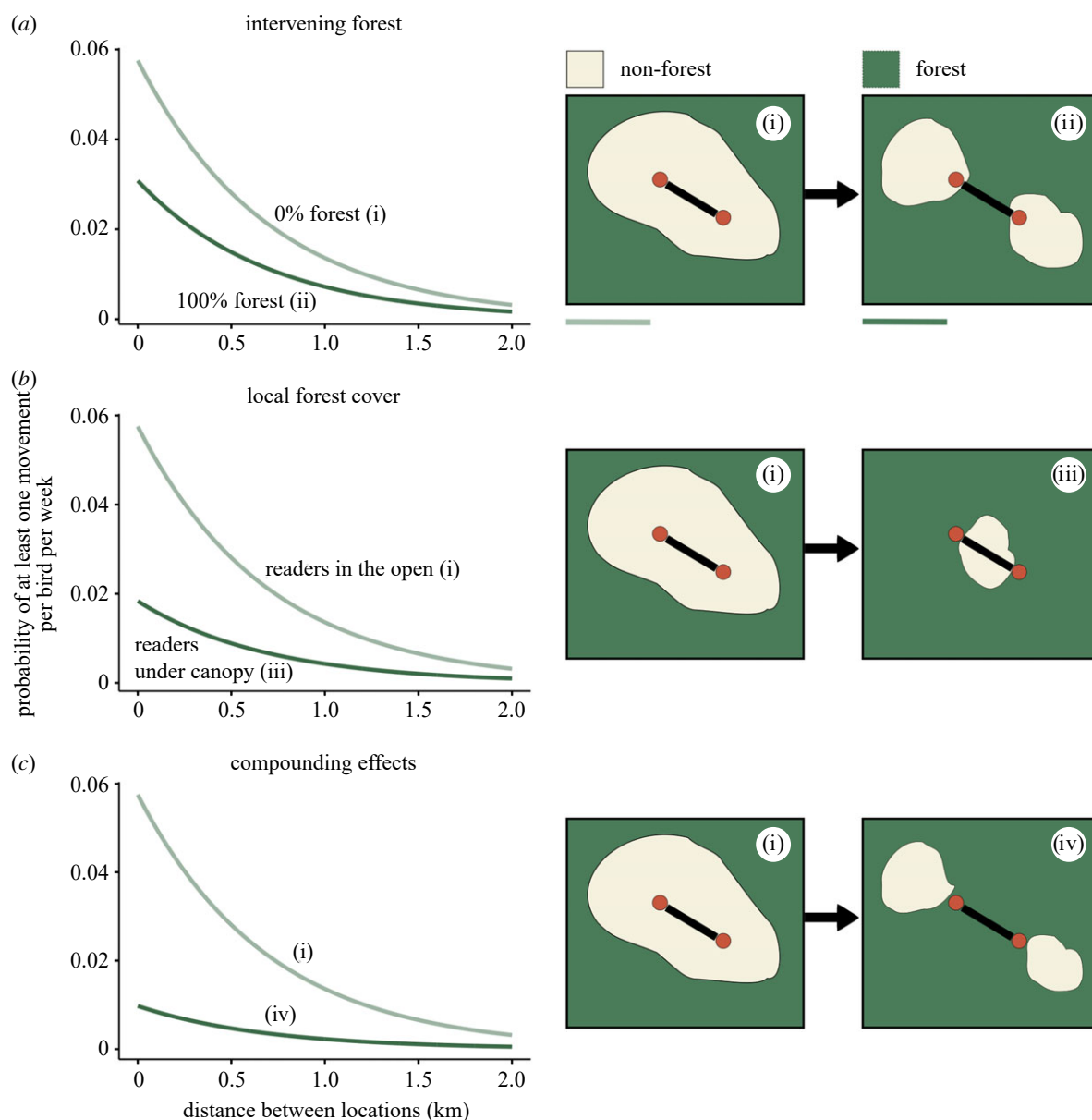
Figure 2. Predicted probability of movement between two food sources with increasing distance and changes in the surrounding landscape. The panels to the right illustrate the change in landscape configuration used to create the line plots. (a) The probability of at least one movement per bird per week (y-axis) between two food sources decreases with increasing distance (x-axis) and is expected to be 45.12% lower if the two locations are isolated by intervening forest (ii). (i) Two food sources in open habitat with 0% intervening forest. (ii) Two food sources in open habitat with 100% intervening forest. (b) (i) Both sources in the open and (iii) both under coniferous forest canopy, holding intervening forest at 0%. (c) (i) Both food sources in the open and (iv) both sources grown over by woody vegetation and separated by 100% forest.

rates from $i \rightarrow j$ tend to be similar to movement rates from $j \rightarrow i$, regardless of the landscape characteristics between or at the locations of i and j.

4. Discussion

We highlight the value of pairing an underutilized passive mark–recapture approach with social network models in the study of foraging patterns of small-bodied organisms (see also [13,18]). We aimed to gain insight into the functional connectivity of high-elevation meadows in the Cascade Mountains in the face of forest encroachment by investigating foraging behaviours of a common pollinator, rufous hummingbirds, in the current landscape. While there remains uncertainty in our estimates of the effects of forest configuration due to a complicated model variance structure and

relatively few recording arrays, our results are most consistent with the *barrier hypothesis*, that pollinator foraging may be limited to open habitat with minimal exploration into or across forested areas. The posterior probabilities that intervening forest and local forest cover have negative effects on hummingbird movement are $P(\beta_{forest} < 0) = 0.811$ and $P(\beta_{cover} < 0) = 0.897$, respectively. Furthermore, the effect sizes (table 1) indicate that increased forest encroachment could substantially reduce the functional connectivity of the landscape (figure 2).

Completely isolating two meadows by increasing the amount of forest in the intervening landscape from 0 to 100% is expected to reduce the background movement rate between them by 45.12% (figure 2a). Similarly, movement between two food sources that are overgrown by woody plants is expected to be 69.27% less than if the two food sources are in the open, holding intervening habitat constant (figure 2b).

Movement rates would be expected to decline by 83.14% between plants at the edge of forest encroachment but in two isolated meadows such that both are overgrown and separated by woody vegetation (figure 2c). Finally, while the high reciprocity in movement rates could help to maintain bidirectional gene flow among subpopulations of hummingbird-pollinated plants, hummingbirds rarely moved farther than 2 km (figures 1d and 2). Further encroachment that increases the gaps among meadows could, therefore, reduce landscape connectivity.

Indeed, supplying artificially high volumes of sucrose at feeders could have reduced the incentive for birds to move among meadows since resource availability is known to influence home range sizes [19]; however, rufous hummingbirds (particularly males) are known to be highly territorial [20], and territoriality often increases at especially valuable resources [21,22]. Thus, it is likely that most birds did not have access to unlimited sugar supplies due to competition at feeders (see supplementary analyses in the electronic supplementary material for more exploration of this hypothesis). This and prior work in similar systems [23] lead us to believe that our results are largely representative of the functional connectivity of the landscape.

Interestingly, all but three movements were by female hummingbirds, even though males were over-represented in the proportion of birds that were relocated following PIT tag implantation (15.1% males implanted, 20.6% of relocated birds were males). Females are known to be less successful in holding territories than males [20], so females may have been forced out of high resource areas, necessitating foraging over greater distances to fulfil energetic requirements. This highlights the potential importance of females in maintaining connectivity among meadows [24] since males are expected to spend more time defending territories, thus moving less, and also migrate early [25], narrowing the window during which they overlap with the flowering period of many plants. However, the relative importance of females over males to functional connectivity may be overstated in our data if experimentally high resource availability resulted in less than average male movement and territory size. Future experiments that focus on explicit measures of pollen flow and pollination efficiency of different pollinator sexes are necessary to test these ideas.

Data on animal movement are ever more available as technologies advance [26,27]. Still, options for automated recording of small-bodied animals remain limited. We illustrate the potential for arrays of feeding stations (or natural forage) equipped with data loggers combined with social network models to provide insight into foraging movements and functional connectivity. From the fitted model, we obtained approximate estimates of foraging range sizes, information supporting frequent out-and-back movements, and tested for landscape resistance to movement. Data such as these may be useful for informing forecasts of the effects of landscape change on populations of plants and animals [28,29]. While considerable uncertainty remains, the posterior mean effect sizes of forest landscape variables suggest that further forest encroachment could substantially reduce pollen flow among ornithophilous plants by acting as a barrier and reducing resource discovery. Finally, if the distance among meadows increases with additional forest encroachment, this could limit foraging among progressively isolated meadows.

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