

Tropical deforestation alters hummingbird movement patterns

Adam S Hadley and Matthew G Betts

Biol. Lett. 2009 **5**, 207-210 first published online 20 January 2009
doi: 10.1098/rsbl.2008.0691

References

This article cites 18 articles, 4 of which can be accessed free
<http://rsbl.royalsocietypublishing.org/content/5/2/207.full.html#ref-list-1>

Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (935 articles)
[behaviour](#) (805 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Biol. Lett.* go to: <http://rsbl.royalsocietypublishing.org/subscriptions>

Tropical deforestation alters hummingbird movement patterns

Adam S. Hadley* and Matthew G. Betts

Department of Forest Ecosystems and Society, Oregon State University,
321 Richardson Hall, Corvallis, OR 97333, USA

*Author for correspondence (adam.hadley@oregonstate.edu).

Reduced pollination success, as a function of habitat loss and fragmentation, appears to be a global phenomenon. Disruption of pollinator movement is one hypothesis put forward to explain this pattern in pollen limitation. However, the small size of pollinators makes them very difficult to track; thus, knowledge of their movements is largely speculative. Using tiny radio transmitters (0.25 g), we translocated a generalist tropical ‘trap-lining’ hummingbird, the green hermit (*Phaethornis guy*), across agricultural and forested landscapes to test the hypothesis that movement is influenced by patterns of deforestation. Although, we found no difference in homing times between landscape types, return paths were on average 459 ± 144 m (\pm s.e.) more direct in forested than agricultural landscapes. In addition, movement paths in agricultural landscapes contained 36 ± 4 per cent more forest than the most direct route. Our findings suggest that this species can circumvent agricultural matrix to move among forest patches. Nevertheless, it is clear that movement of even a highly mobile species is strongly influenced by landscape disturbance. Maintaining landscape connectivity with forest corridors may be important for enhancing movement, and thus in facilitating pollen transfer.

Keywords: animal movement; translocation; connectivity; pollination; ecosystem services

1. INTRODUCTION

Recent research shows global declines in plants and associated pollinators (e.g. Biesmeijer *et al.* 2006), sparking concerns about a widespread pollination crisis. The causes of these declines remain obscure, but habitat loss and fragmentation are expected to be primary drivers since pollen is often limited in fragmented landscapes (Aguilar *et al.* 2006; Steffan-Dewenter & Westphal 2008). Unfortunately, the specific mechanisms for pollen limitation remain largely unknown. Three hypotheses have been forwarded to explain pollen limitation as a function of habitat loss and fragmentation. First, landscape disturbance may negatively affect plant abundance, density and health, thereby reducing the total amount of pollen available for transfer (de Blois *et al.* 2002). Second, the abundance, distribution and diversity of pollinators upon which plants depend may be reduced by landscape disturbance (Steffan-Dewenter & Westphal 2008). Finally, disturbance may restrict the movements

of pollinators, thus reducing their effectiveness in pollen transfer (Tewksbury *et al.* 2002). Despite the potential for direct effects of animal movement decisions on pollination, the pollinator movement hypothesis has received little attention due to the inherent difficulties in tracking small pollinators (Ghazoul 2005).

Previous work has shown continued persistence of several hummingbird species in fragmented tropical landscapes (Stouffer & Bierregaard 1995). Taken superficially, this could imply that plant species reliant on hummingbird pollinators should show minimal pollen limitation; however, hummingbird persistence at the landscape scale does not imply that all patches in a landscape will be visited frequently, or that inter-patch pollen transfer will occur. Pollen transfer is determined by whether landscapes facilitate or impede pollinator movements between resource patches (i.e. its ‘functional connectivity’; Bélisle 2005). Indeed, varying costs associated with different landscape elements (e.g. patches, matrix, corridors; Forman 1983) are hypothesized to affect animal movement decisions (Lima & Zollner 1996).

Experimental manipulations, such as translocations and precise tracking methods, are thought to provide meaningful measures of functional connectivity; the rates and paths of animal return to territorial patches provide measures of landscape resistance (Bélisle 2005). Our research capitalized on recent advances in miniaturization of animal tracking technology (e.g. Wikelski *et al.* 2006) that, along with a translocation approach, allowed us to test the hypothesis that hummingbird movement is altered by tropical deforestation.

We investigated the effects of tropical forest conversion to agriculture on movements of the green hermit (*Phaethornis guy*), a generalist forest trap-lining species. We selected a trap-liner because they acquire necessary resources from isolated nectar-rich flowers over relatively large spatial scales, a strategy that precludes territoriality (Stiles 1975). We chose a generalist species because changes in its movements will probably have broader ecological impacts than in the case of more specialized pollinators (Ghazoul 2005). Generalist pollinators affect a large number of plant species, particularly pollinator specialized plants which often depend exclusively on generalist pollinators for pollen transfer (Bascompte *et al.* 2006). Green hermits are forest-dependent, but persist in fragmented landscapes, making them ideal for comparing movements between altered and intact landscapes.

We compared the functional connectivity of primarily agricultural versus forested landscapes. If deforestation impedes hummingbird movements, we expected longer homing times and/or limited homing success in agricultural relative to forested landscapes. Second, if hummingbirds take detours and avoid crossing open pastureland while homing, movements through agricultural landscapes should be longer and less direct than those taken through forest. Third, we expected homing paths in agricultural landscapes to be characterized by greater forest cover in comparison to the most direct routes to capture locations.

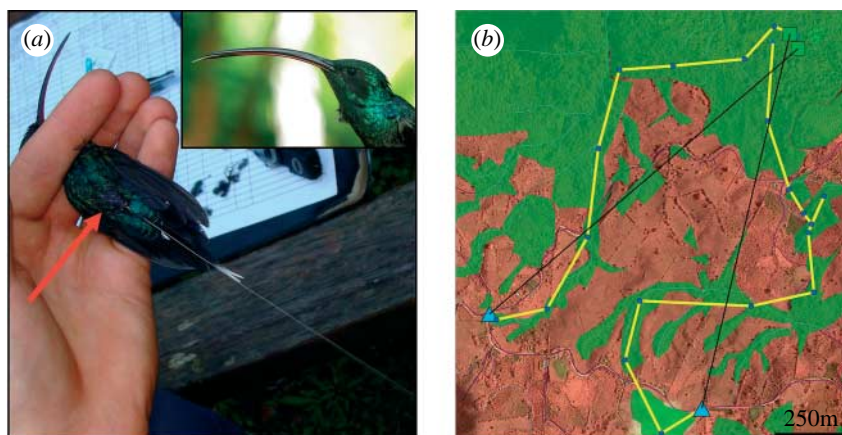


Figure 1. (a) An adult green hermit (*P. guy*; inset) and the same species with a transmitter attached for monitoring movements. (b) An example of two hummingbird movement paths through agricultural landscapes. Movement paths are shown in yellow with telemetry locations in blue. Direct-line distances between release (blue triangles) and capture locations (green squares) are shown in black. Forested areas are in green, agriculture in brown. Photo credits: J. Miller (a), M. Betts (b).

2. MATERIAL AND METHODS

(a) Study site

We conducted the study at the organization for tropical studies, Las Cruces Biological Station, Costa Rica (8°47' N, 82°57' W). The site contains a 235 ha reserve comprising primary and old secondary forest. The surrounding agricultural matrix was previously forested, but now is dominated by pasture and shade coffee plantations. Remaining fragments of Pacific premontane humid forest (1–82 ha) and forested riparian corridors (10–40 m wide) are scattered throughout this agricultural landscape.

(b) Telemetry and translocations

We captured 19 green hermits (8 male, 11 female) January 30–March 9, 2008 and fitted them with radio-telemetry units (0.25 g, Blackburn Transmitters, figure 1). The relatively large size of this species (5.8 ± 0.09 g), made it a logical first test of using telemetry to monitor hummingbird movements. We used eyelash glue to attach transmitters to plucked bare skin on the lower backs of birds. Transmitters fell off very rapidly (approx. two weeks) once the feathers began to re-grow. Hummingbirds appeared to have no difficulty flying with the radio-tags; we observed no behavioural differences between tagged and untagged individuals. In one instance, we observed a tagged female chasing off an untagged individual during a territorial dispute.

We translocated ten hummingbirds through continuous forest and nine across agricultural landscapes. We maximized differences between forested and agricultural treatments by translocating birds across agricultural landscapes with less than 50 per cent residual forest. Hummingbirds were transported 340–1500 m, providing a range of distances that allowed us to test the effect of scale on homing efficiency. Translocations were conducted between 06.00 and 15.00; no results were influenced by time of day ($p > 0.4$). We placed hummingbirds in cloth bags and transported them by foot or vehicle depending on terrain. Release points were dictated, to a certain extent, by roads and trails to minimize handling time (less than 40 min). We alternated translocation distance (less than 1000/more than 1000 m) and landscape type (agriculture/forest).

We recorded homing times for returning individuals and the movement paths they used. We followed birds as closely as possible on foot (less than 200 m) using two teams with radio receivers and handheld Yagi antennae. Bird locations were recorded whenever a position could be determined to within 50 m (mean = 8 points/bird, range 4–14; short-distance translocations had fewer locations). Based on trials under optimal conditions with known transmitter distances, we assumed that a bird was within 50 m whenever signal strength was 0.4 (gain less than 1/2). A bird was considered to have successfully homed when it was relocated within 50 m of the capture location.

(c) Analysis

We calculated the effects of landscape type on home time, difference in path length and fractal dimension using generalized linear models with a Gaussian distribution. We used fractal dimension to measure path tortuosity (i.e. the degree of twisting

and turning). Fractal dimension (D) was calculated as: ($D = \log(n) / (\log(n) + \log(d/L))$), where L = total path length; d = length of line segment; and n = number of segments). Number of segments was included in all GLMs containing D in order to account for the different number of spatial locations collected for each path. To determine if birds selected forest when moving through agricultural landscapes, we calculated the proportion of forest within 30 and 100 m diameter buffers around the movement paths of each individual (i.e. 'observed') and around the shortest distance between capture and release points (i.e. 'available'). The 30 m buffer reflects the average width of linear forest strips within study area agricultural landscapes. Since our forest data were not normally distributed, we tested for differences between observed and available proportions of forest using Exact Wilcoxon signed-rank tests. We used R (v. 2.7.1) for all statistical tests. In all analysis, we report the mean differences \pm s.e.

3. RESULTS

All but one individual homed successfully within 4 hours of release, even over translocation distances up to 1500 m. The single individual that failed to return home (translocated 1300 m across an agricultural landscape) was excluded from all analyses. We detected no difference in homing times between agricultural and forested landscapes (difference in means = 9.7 ± 22 min, $F = 0.73$, $n = 18$, $p = 0.71$, figure 2a). However, homing paths of birds in agricultural landscapes were 459 ± 144 m longer ($F = 10$, $n = 18$, $p = 0.006$, figure 2b, (forest 153 ± 70 m, agriculture 544 ± 129)) and more tortuous (0.230 ± 0.013 , $F = 9.6$, $n = 18$, $p = 0.007$, (forest 1.12 ± 0.04 , agriculture 1.4 ± 0.08)) than those through contiguous forest.

Hummingbirds tended to associate with forest remnants when homing through agricultural landscapes. Movement paths of homing individuals contained 36 ± 4 per cent more forest than if they had taken the most direct route (30 m buffer; $W = 0$, $p < 0.01$, $n = 8$). At the 100 m buffer scale, paths contained 68 ± 4 per cent more forest ($W = 0$, $p < 0.01$, $n = 8$).

4. DISCUSSION

Green hermits appear to have excellent homing capacities, even in heavily deforested landscapes. Contrary to our expectations and unlike several

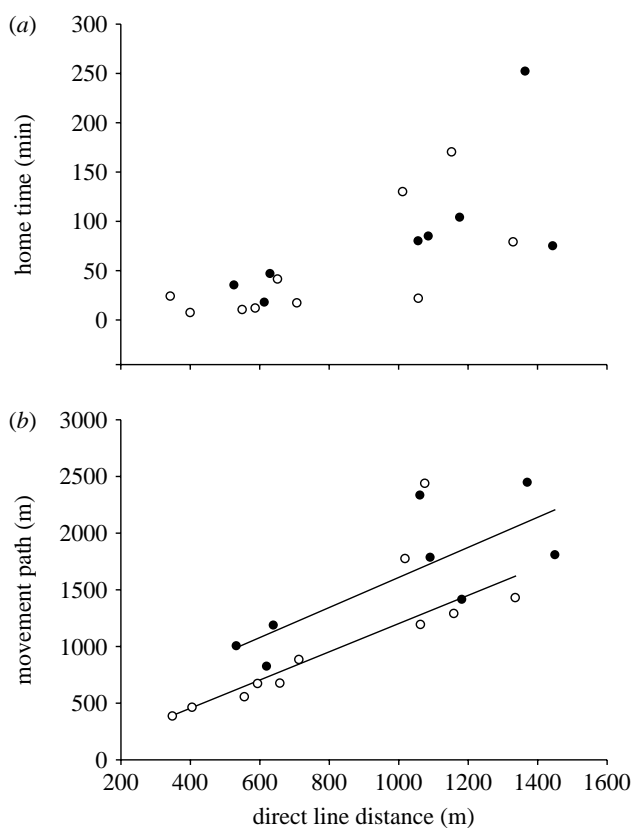


Figure 2. (a) Homing times for 18 green hermits translocated across agricultural and forested landscapes. (b) The directness of homing movements for birds translocated across agricultural and forested landscapes. Filled circles, agriculture; open circles, forest.

previous translocation studies (e.g. B elisle *et al.* 2001), homing times did not depend on whether landscapes were primarily forested or agricultural. In both landscape types, birds returned within 4 hours even when translocated up to 1500 m. This is congruent with previous studies showing relatively high vagility of a *Phaethornis* hummingbird species (Moore *et al.* 2008).

However, the paths selected by hummingbirds to traverse intervening landscapes revealed that deforested gaps alter movement pathways. In agricultural landscapes, birds moved longer distances and took more circuitous routes than in forested landscapes. Overall, movement paths were strongly biased towards areas with higher forest cover. Although this does not represent the extreme gap crossing avoidance shown by some other tropical species (Stratford & Stouffer 1999; Moore *et al.* 2008), it does show that even highly mobile species can be influenced by fragmentation. An agricultural matrix may increase the vulnerability of hummingbirds to predators at forest edges. Animal movements are often influenced by perceived risk of predation even if the probability of mortality is low (Lima & Zollner 1996).

We show that even a generalist species with high vagility avoids crossing open matrix in favour of longer forested detours. Asymmetric coevolution of pollination networks has resulted in the reliance of many plants on generalist pollinators as their sole source of pollen (Bascompte *et al.* 2006). Changes in movement patterns as a function of landscape context

could thus have profound impacts on pollen movement (Steffan-Dewenter & Westphal 2008) and therefore the persistence of many plant species.

Our work adds to a growing body of evidence for the importance of remnant forest strips and riparian buffers (i.e. corridors) in highly modified landscapes (Tewksbury *et al.* 2002; Hawes *et al.* 2008). Maintenance of forest along hedgerows or streams will probably facilitate inter-patch movements and should be important for pollen transfer events. We predict that fidelity to linear forest habitats by hummingbird pollinators could 'scale up' to result in fragmentation effects on plant demography that are independent of the detrimental influence of habitat loss (Fahrig 2003).

We thank C. Mendenhall, C. Sekercioglu and the Las Cruces Biological Station for site access and assistance with the project. B. Zitske, S. Gullage, M. Hadley and C. Moreno provided valuable field assistance. J. Rivers, S. Shirley and S. Frey provided helpful comments. A.H. was funded under a National Science and Engineering Council of Canada (NSERC) PGS D.

- Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M. A. 2006 Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecol. Lett.* **9**, 968–980. (doi:10.1111/j.1461-0248.2006.00927.x)
- Bascompte, J., Jordano, P. & Olesen, J. M. 2006 Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* **312**, 431–433. (doi:10.1126/science.1123412)
- B elisle, M. 2005 Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* **86**, 1988–1995. (doi:10.1890/04-0923)
- B elisle, M., Desrochers, A. & Fortin, M. J. 2001 Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* **82**, 1893–1904. (doi:10.2307/2680055)
- Biesmeijer, J. C. *et al.* 2006 Parallel declines in pollinators and insect-pollinated plants in Britain and The Netherlands. *Science* **313**, 351–354. (doi:10.1126/science.1127863)
- de Blois, S., Domon, G. & Bouchard, A. 2002 Landscape issues in plant ecology. *Ecography* **25**, 244–256. (doi:10.1034/j.1600-0587.2002.250212.x)
- Fahrig, L. 2003 Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515. (doi:10.1146/annurev.ecolsys.34.011802.132419)
- Forman, R. T. T. 1983 An ecology of the landscape. *Bioscience* **33**, 535.
- Ghazoul, J. 2005 Pollen and seed dispersal among dispersed plants. *Biol. Rev.* **80**, 413–443. (doi:10.1017/S1464793105006731)
- Hawes, J., Barlow, J., Gardner, T. A. & Peres, C. A. 2008 The value of forest strips for understory birds in an Amazonian plantation landscape. *Biol. Conserv.* **141**, 2262–2278. (doi:10.1016/j.biocon.2008.06.017)
- Lima, S. L. & Zollner, P. A. 1996 Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* **11**, 131–135. (doi:10.1016/0169-5347(96)81094-9)
- Moore, R. P., Robinson, W. D., Lovette, I. J. & Robinson, T. R. 2008 Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecol. Lett.* **11**, 960–968. (doi:10.1111/j.1461-0248.2008.01196.x)

- Steffan-Dewenter, I. & Westphal, C. 2008 The interplay of pollinator diversity, pollination services and landscape change. *J. Appl. Ecol.* **45**, 737–741. (doi:10.1111/j.1365-2664.2008.01483.x)
- Stiles, F. G. 1975 Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* **56**, 285–301. (doi:10.2307/1934961)
- Stouffer, P. C. & Bierregaard, R. O. 1995 Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. *Conserv. Biol.* **9**, 1085–1094. (doi:10.1046/j.1523-1739.1995.9051085.x)
- Stratford, J. A. & Stouffer, P. C. 1999 Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conserv. Biol.* **13**, 1416–1423. (doi:10.1046/j.1523-1739.1999.98494.x)
- Tewksbury, J. J. *et al.* 2002 Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl Acad. Sci. USA* **99**, 12 923–12 926. (doi:10.1073/pnas.202242699)
- Wikelski, M., Moskowitz, D., Adelman, J. S., Cochran, J., Wilcove, D. S. & May, M. L. 2006 Simple rules guide dragonfly migration. *Biol. Lett.* **2**, 325–329. (doi:10.1098/rsbl.2006.0487)