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*Research Paper*

# Functional connectivity of managed forest landscapes for the Ovenbird: an experimental assessment of within-patch movement behavior

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ABSTRACT. Conservation efforts addressing the impacts of habitat loss and fragmentation on movements must rely on operational definitions of land-cover types that are relevant to the behavioral decisions made by the species of interest. Travel costs, and ultimately landscape resistance (or permeability to movement) can be assessed through experiments standardizing the motivation of individuals to move across specific landscape elements, including habitat patches, the matrix, and their edges. So far, most studies modeling landscape permeability based on cost values have focused on habitat-specialist species and characterized landscape composition based on contrasting, human-defined cover types such as forest and open land. We experimentally evaluated the permeability to movement of different forest-cover types for the Ovenbird (*Seiurus aurocapilla*), a neotropical migratory species breeding in mature deciduous or mixed forest. We compared homing time and movement patterns of 60 radio-tracked males translocated over 500 m and released in untreated or partially harvested mature deciduous stands, as well as in conifer plantations, in northwestern New Brunswick, Canada. Although there was no strong effect of forest-cover type on homing time, path tortuosity, or travel speed, individuals released in conifer plantations tended to move faster and straighter than those released within untreated forest. Considering that translocated Ovenbirds have been shown to be less likely to return to capture sites in landscapes dominated by conifer plantations, our results suggest that they minimize time spent in inhospitable cover types. Responses to conifer plantation edges and similar interfaces may thus represent decisive components of time-based functional connectivity estimates. Hence, it appears that not all forest-cover types offer an equal resistance to Ovenbird movements and, consequently, a dichotomic habitat/non-habitat view may be too simplistic when assessing or modeling landscape permeability for passerine birds.

## Connectivité fonctionnelle de paysages forestiers sous aménagement: évaluation expérimentale des mouvements de la Paruline couronnée à l'intérieur de parcelles

RÉSUMÉ. Les stratégies de conservation visant à réduire les impacts de la perte et de la fragmentation de l'habitat sur les mouvements doivent reposer sur des définitions opérationnelles des types de milieux qui sont pertinentes aux décisions prises par les individus des espèces focales. Les coûts de déplacement et, ultimement, la résistance du paysage (ou perméabilité au mouvement), peuvent être estimés par le biais d'expérimentations permettant de standardiser la motivation des individus à se déplacer à travers des composantes spécifiques du paysage, incluant les parcelles d'habitat, la matrice et leurs bordures. Jusqu'à maintenant, la plupart des études ayant modélisé la perméabilité du paysage à partir d'estimations de coûts se sont concentrées sur des espèces spécialistes en termes d'utilisation de l'habitat et ont caractérisé les paysages selon une perspective anthropique fondée sur des types de milieux contrastants, tels les forêts et les milieux ouverts. Nous avons évalué expérimentalement la perméabilité de différents types de couvert forestier aux mouvements de la Paruline couronnée (*Seiurus aurocapilla*), un migrateur néotropical qui niche dans les peuplements matures feuillus ou mixtes. Par des suivis télémétriques, nous avons comparé les temps de retour et les patrons de mouvement de 60 mâles déplacés sur 500 m et relâchés au sein de parcelles de forêt feuillue mature non-aménagée ou partiellement exploitée et de plantations de conifères dans le nord-ouest du Nouveau-Brunswick, au Canada. Malgré l'absence d'un effet important du type de couvert forestier sur le temps de retour, la tortuosité des trajets ou la vitesse de déplacement, les individus relâchés au sein des plantations de conifères avaient tendance à se déplacer plus rapidement et plus directement que lorsque relâchés au sein de peuplements forestiers non-aménagés. Puisqu'il a été montré que la Paruline couronnée est moins susceptible de revenir au site de capture lorsqu'elle doit traverser un paysage dominé par les plantations de conifères, nos résultats suggèrent qu'elles tentent de minimiser le temps passé au sein des types de couvert inhospitaliers. La réponse des individus aux bordures des plantations de conifères et aux autres interfaces similaires pourrait ainsi représenter une composante cruciale de l'estimation de la connectivité fonctionnelle. Il semblerait que les différents types de couvert forestier n'offrent pas tous une résistance égale aux mouvements de la Paruline couronnée. Il s'ensuit qu'une vision dichotomique habitat/non-habitat pourrait être trop simpliste pour l'évaluation ou la modélisation de la perméabilité des paysages aux mouvements des passereaux.

Key Words: *dispersal; functional connectivity; habitat fragmentation; homing; matrix resistance; Seiurus aurocapilla; spatial ecology*

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# INTRODUCTION

Landscape structure influences the movements of organisms at a range of spatial scales and, thus, plays a crucial role in the selection and use of habitats, and ultimately, population dynamics (Bélisle 2005, Lindenmayer and Fischer 2006). For instance, dispersal can be costly for individuals inhabiting highly fragmented landscapes (Matthysen and Currie 1996, Doherty and Grubb 2002, Clobert et al. 2012) and, patch occupancy and colonization rates tend to be lower in those landscapes (Villard et al. 1995, Pavlacky et al. 2012). This is not without consequences because such patterns can alter gene flow and rescue effects and, ultimately, population persistence, community structure, and eco-evolutionary dynamics (Hanski 1999, Pelletier et al. 2009, Callens et al. 2011, Haddad et al. 2015).

Functional connectivity, "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993:571), integrates the behavioral responses of individuals to landscape structure. Hence, this landscape property is species- and context-specific (Taylor et al. 1993, Bélisle 2005). To properly address the impacts of habitat loss and fragmentation on movements, conservation planners must therefore rely on an adequate definition of resource patches, on information regarding the selection, use and quality of those patches at different spatial and temporal scales, and on an appropriate measure of functional connectivity, and this, for different species in different behavioral contexts (e.g., Callens et al. 2011). Hence, the challenge lies partly in mapping the landscape as seen through the eyes of focal species rather than through those of researchers or their instruments, because functional connectivity is expected to reflect the amount and spatial organization of land-cover types as perceived by the former (Jonsen and Taylor 2000, Betts et al. 2014, Villard and Metzger 2014).

Despite the lack of consensus regarding how to quantify functional connectivity (Bélisle 2005, Betts et al. 2015), some experimental methods that standardize the motivation of individuals to move within or across specific landscape elements or structures appear to be appropriate to obtain indirect estimates of this landscape parameter (reviewed by Bélisle 2005). Such proxies include homing time and probability following a translocation (e.g., Bélisle et al. 2001, Gobeil and Villard 2002) and movement probability when lured toward a given location, i.e., "gap crossing" (e.g., Rail et al. 1997, St. Clair et al. 1998). From these quantitative estimates, it is common practice to derive a travel cost associated with moving across specific land-cover types (Desrochers et al. 2011, Zeller et al. 2012). Despite some potential biases (Betts et al. 2015), the translocation of site-tenacious individuals is increasingly recognized as a suitable approach to infer functional connectivity (e.g., Smith et al. 2013, Fletcher et al. 2014, St-Louis et al. 2014, Betts et al. 2015, Nowakowski et al. 2015). Depending on the spatial scale of the experiment, it is possible to collect precise homing times and to document movement paths by following translocated individuals using tracking technologies (e.g., Hadley and Betts 2009, Aben et al. 2012, Volpe et al. 2014, Valente et al. 2019). Several indices can then be derived from a movement path to characterize movement behavior, most of which focus on its tortuosity (Almeida et al. 2010).

Travel costs between two points, also referred to as landscape resistance to movement, can be quantified by adding up resistance values attributed to each land-cover type present in the intervening landscape (Adriaensen et al. 2003). These values are either determined based on expert knowledge, field data (such as movement paths or probabilities), model optimization, or a combination thereof (e.g., St-Louis et al. 2014). Although the most accurate source of information is generally field data, studies based on empirically derived resistance values are uncommon, probably because they are notoriously time consuming to conduct (Spear et al. 2010).

Most studies modeling landscape permeability based on cost values have focused on forest bird species and have only considered two land-cover types, i.e., the presence or absence of forest cover (e.g., Desrochers et al. 2011, St-Louis et al. 2014, Rayfield et al. 2016). This simple land-cover classification probably stems from the fact that many forest-dwelling bird species avoid crossing open areas outside of migration periods (e.g., Desrochers and Hannon 1997, Robichaud et al. 2002, Awade and Metzger 2008, Ibarra-Macias et al. 2011, Valente et al. 2019), possibly as a result of perceived predation risk (Lima and Dill 1990, Zollner and Lima 2005). The fact that woodland birds often follow forest edges when facing open areas (Desrochers and Fortin 2000, Bélisle and Desrochers 2002) led to the attribution of high resistance values to such sharp ecotones. However, bird movements across softer edges, such as those separating forest stands of contrasting tree-species composition or structure, have received much less attention. This issue has both theoretical and practical relevance, considering the worldwide increase in area devoted to intensive forestry and tree plantations (FAO 2010). Indeed, although some authors suggest that tree plantations may enhance connectivity under certain conditions (Brockerhoff et al. 2008, Nogués and Cabarga-Varona 2014), others have shown that this cover type can impede movements (Villard and Haché 2012, Mortelliti et al. 2014, Knowlton et al. 2017). Knowlton et al. (2017) radio-tracked translocated birds through forested landscapes including oil palm plantations and found that individuals seemed to take longer routes to avoid this anthropogenic cover type. If some forest-cover types of anthropogenic origin are indeed less permeable or avoided by moving individuals, then they should be distinguished from forest-cover types considered as habitat to improve estimates of functional connectivity.

The aim of this study was to experimentally evaluate the permeability to movement of different forest-cover types for a forest specialist, the Ovenbird (*Seiurus aurocapilla*). We compared homing time and movement patterns of translocated individuals released in three cover types: untreated mature deciduous stands, partially harvested mature deciduous stands, and conifer plantations. The Ovenbird is a neotropical migrant that tends to avoid moving across open land, including agricultural fields and clearcuts, during the breeding season (Bélisle et al. 2001, Gobeil and Villard 2002, Robichaud et al. 2002, Valente et al. 2019). Translocation data also suggest that this species is reluctant to move across forest edges facing conifer plantations (Villard and Haché 2012), possibly because their structure contrasts with that of its breeding habitat (Porneluzi et al. 2020). We predicted that individuals released within untreated mature deciduous stands would exhibit slower and more sinuous movements than those released in conifer plantations because search and foraging behavior are expected to be more frequent in the former (Van Dyck and Baguette 2005, Barraquand and Benhamou 2008). Birds released in conifer plantations were expected to show a straighter trajectory and faster pace, as expected from individuals attempting to leave an inhospitable land cover (Doncaster et al. 2001, Goodwin and Fahrig 2002, Haynes and Cronin 2006, Delattre et al. 2010, Brown et al. 2017), resulting in shorter homing time. Finally, we expected similar results for both deciduous cover types because tree species composition was similar and partially harvested stands only had narrow (5 m) harvest trails, which are not expected to slow down the movements of forest passerine birds (Bélisle and Desrochers 2002, Turcotte and Desrochers 2003).

# METHODS

## Study area and experimental design

Field work was conducted in the summers of 2015 and 2016 in northwestern New Brunswick, Canada (47°29′00.0″ N, 68°07′00.0″ W; see Geoffroy et al. 2019 for a detailed description of the study area). All capture sites were composed of mature deciduous-dominated forest stands and were adjacent to the forest-cover type being tested. Birds were translocated to one of nine release areas corresponding to one of three forest-cover types: untreated mature deciduous forest stands, partially harvested mature deciduous forest stands, and conifer plantations, for a total of three release areas per cover type. The three release areas in untreated mature deciduous stands (hereafter untreated forest) had the same tree species composition as capture sites. Three release areas had been subjected to a partial harvest treatment in the last 10 years. This treatment consisted of clearcutting 5-m wide harvest trails while leaving 18 to 20-m wide strips of partially harvested, mature deciduous-dominated forest between them (30-40% basal area removal). Trails were mostly parallel and had < 2.5 m-high regeneration. Finally, the three release areas in conifer plantations were composed of ~40-year-old white spruce (*Picea glauca*), sometimes mixed with black spruce (*P. mariana*), with scattered balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*). All release areas were selected based on their tree species composition (as homogeneous as possible within a given area as well as among areas of a given cover type), their area (large enough to allow ~6 replicate 500-m translocations), and their proximity to a stand of untreated, mature deciduous-dominated forest large enough to host ≥ 6 Ovenbird territories.

## Translocation protocol

Translocations were performed between 1-6 June 2015 and between 23 May and 20 June 2016. Territorial males were captured between 0602 and 1008 (AST) using conspecific playbacks and a mist net. We started the experiment approximately 10 days after the first sighting of a singing male in the study area to ensure that territories would be firmly established and that males would exhibit homing behavior following their translocation (Gobeil and Villard 2002, Villard and Haché 2012, Geoffroy et al. 2019). Upon capture, birds were fitted with a unique combination of an aluminum band and one color band on each leg, and a VHF transmitter (0.5 g, Advanced Telemetry Systems, Isanti, Minnesota) using a harness made of elastic nylon strings (Streby et al. 2015). Prior to release, we recorded handling time, i.e., the time elapsed between capture and release (mean ± SD; 82 ± 19 min, max = 146 min), to control for its potential influence on homing time.

Birds were placed in an opaque cotton bag and carried to the release site by foot as fast as possible. For cover types that were separated from capture sites by an edge, namely spruce plantation and partially harvested deciduous forest (hereafter partially harvested forest), each observer started walking from the capture site (within untreated forest) perpendicularly to the edge and recorded the distance traveled to that point. From the edge, the observer then walked an additional 500 m along the same axis, released the individual, and immediately started tracking its movements. In untreated forest stands, the observers simply walked 500 m along a compass bearing directed away from the capture site. This methodology made it possible to track individuals over the same potential distance (i.e., 500 m) for different cover types. Warblers can perform extra-territorial movements of up to 2.5 km to seek partners (Norris and Stutchbury 2001) and the average territory size of an Ovenbird in our study region is ca. 1 to 1.27 ha (56 to 64 m radius; Haché and Villard 2010). Considering that 50% of Ovenbirds translocated over 5.9 ± 0.4 km in the same study area returned to their territories within less than 48 hours (Geoffroy et al. 2019), we assumed that such differences in total translocation distance among treatments (conifer plantations: 120 ± 100 m; partially harvested stands: 130 ± 125 m) were negligible with respect to their effect on homing capacity and motivation.

Birds were followed by foot until they returned to the vicinity of the capture site (Figs. 1, 2; Appendix 1, Figs. A1.1-A1.7). Otherwise, observations were terminated after five hours of tracking and birds were considered not returned. Efforts were made to avoid flushing the individuals while following them and movement paths were recorded by taking a geographical location with a GPS every 5 minutes when the bird was not moving or walking slowly, or every time the observer was confident that a moving bird was within 30 m, based on the strength of the signal. When birds where moving more rapidly, positions were taken at a higher rate, unless the movement of the individual covered a long distance and the observer needed more time to catch up and find the bird. Homing was considered successful when an individual arrived within 50 m from its capture site, when released in untreated forest, or when it reached the untreated forest edge, when released in one of the other forest-cover types. An observer with a receiver and antenna remained near capture sites to confirm homing success in cases where the tracking observer lost the signal. Only birds that had precise return times or were tracked successfully for five hours, if they did not return to their capture site, were included in the analyses.

Translocations were not performed under rainy conditions and we alternated cover types and capture sites to make sure that they were equally distributed over the duration of the experiment. Birds were caught no later than 1007 a.m. to try to minimize the impact of time of the day on their level of activity. Even though transmitters are known to fall off within 40 to 70 days following installation (Streby et al. 2015), we attempted to recapture most of the individuals that homed successfully within 14 days (> 70% of translocated individuals) and were able to retrieve 42% of the units.

**Fig. 1**. Paths taken by Ovenbird (*Seiurus aurocapilla*)individuals following experimental translocation over ~500 m in untreated mature deciduous forest (site G). Release sites are shown only for non-returned individuals to indicate movement direction. Capture sites are shown if different from arrival and for non-returned individuals. Return times (min.) are shown next to arrival. Homing was considered successful when an individual arrived within 50 m from its capture site.

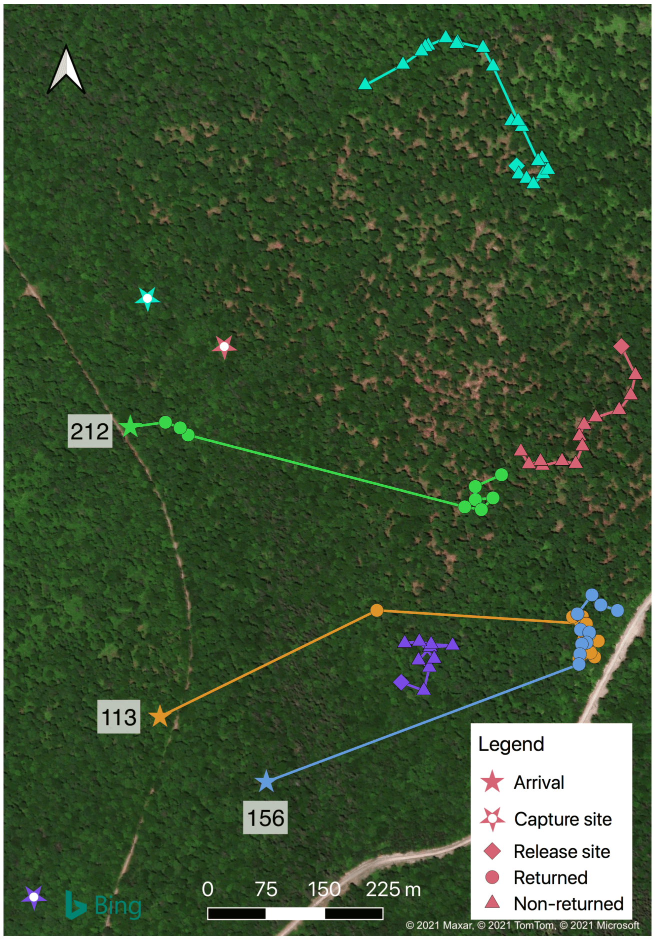
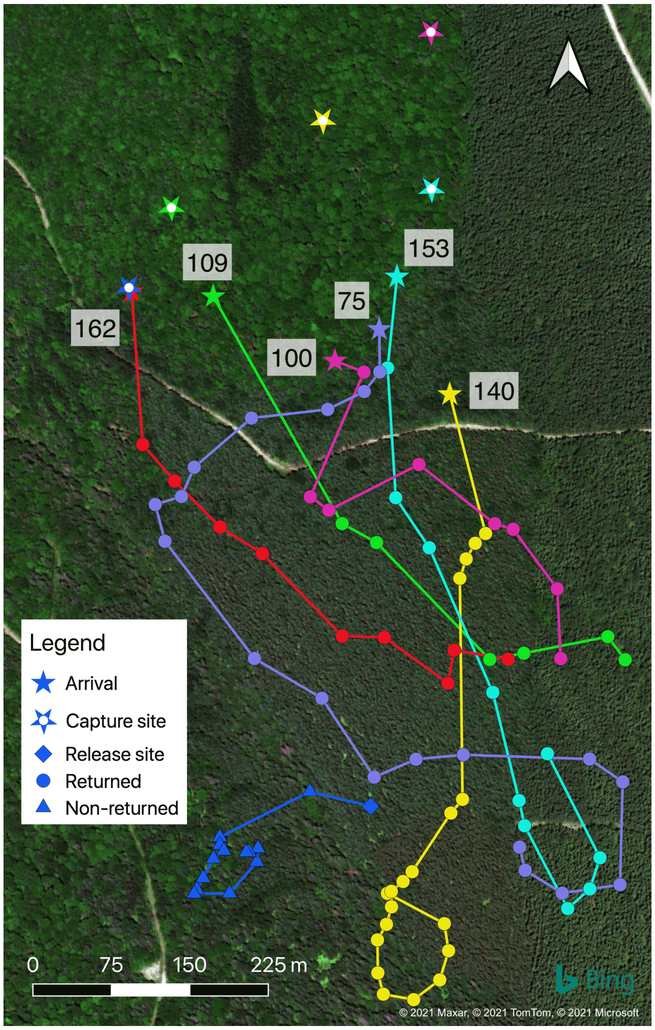


**Fig. 2**. Paths taken by translocated Ovenbirds (*Seiurus aurocapilla*) captured in untreated mature deciduous forest and released ~500 m away in conifer plantation (site J). Release sites are shown only for non-returned individuals to indicate movement direction. Capture sites are shown if different from arrival and for non-returned individuals. Return times (min.) are shown next to arrival. Homing was considered successful when individuals reached the untreated forest edge.



## Differences in homing time

To assess the influence of forest-cover type on homing time, we used Cox proportional hazards mixed regression models (Therneau and Grambsch 2000). We treated birds that did not return as singly Type I, right-censored data (sensu Allison 1995) and fitted our models in R v. 3.2.3 (R Core Team 2015) with the “coxme” package (Therneau 2015*a*) and Efron’s approximation. Proportional hazards assumption was verified based on weighted residuals using the “cox.zph” function of the “survival package” (Grambsch and Therneau 1994, Therneau 2015*b*).

We assessed the influence of forest-cover type on homing time by comparing the fit of two models: one comprising only cover type as the explanatory variable and one null (intercept-only) model. Both models included “release area” as a random effect to account for the fact that several birds were released into one of three areas for each cover-type treatment. We elected not to include potential confounding variables, such as handling time, Julian day, or time of capture. These variables showed overlapping distributions among cover types (Appendix 1: Figs. A1.8-A1.10) and had no effect on the homing time of territorial male Ovenbirds translocated over 6 km in the same area (mean handling time: 77 ± 23 min, max = 148 min; Geoffroy et al. 2019), suggesting that they would not bias the effect of cover type on homing time. We also decided not to include pairing status because it would have been a major challenge to determine for a large number of individuals. Moreover, Gobeil and Villard (2002), who translocated territorial male Ovenbirds over 1.5 to 2.7 km during the same period of the breeding season, reported that it had no effect on return rates.

Finally, we used the second-order Akaike's information criterion (AICc; Burnham and Anderson 2002) to rank our models with R v. 3.2.3 (R Core Team 2015) and the "AICcmodavg" package (Mazerolle 2016). We also calculated a 95% confidence interval for the effect of each forest-cover type.

## Differences in homing movement patterns

We characterized homing movement patterns based on two indices: an index of path tortuosity, the inverse straightness index (IST), and global speed. We used IST, which is simply the inverse ratio of the straightness index (ST), to facilitate the interpretation. The ST is defined as the Euclidean distance between the release and capture sites (d) divided by the total length of the path followed by the individual (Batschelet 1981). Hence, the closer the IST is to 1, the straighter the path is, with greater values indicating higher levels of tortuosity. This index should not be highly sensitive to the number of locations taken given the spatial scale involved and the fact that observers were usually able to capture the positions of the birds before and after each path segment of significant length within a relatively short time. In the event that birds moved very fast, it is very unlikely that they moved tortuously and hence, that they deviated from a more or less straight line, especially because they were as a rule closely followed by the observer or detected by the observer at the capture site. Simulations have shown ST to be a reliable index of the efficiency of oriented movements induced by homing experiments (Benhamou 2004, Almeida et al. 2010). Global speed (m/min) was defined as the total path length divided by the total time elapsed between release and arrival, or five hours if the individual had not yet returned to the capture site. Birds that did not have a complete sequence of geographical locations were not included in the analysis. To investigate the possible lack of independence between IST and global speed, we assessed their association using Kendall's correlation coefficient while accounting for ties.

To compare homing movement patterns between forest-cover types, we elected not to perform mixed models given that limited replication can lead to estimation problems (Gelman and Hill 2007, Bolker et al. 2009). We therefore used the most powerful alternative (Bolker 2008) and performed hierarchical randomization tests where treatment (cover type) was randomly attributed to each release area while conserving the hierarchical structure of the experimental design where birds were nested within release areas. Considering that this approach is conservative and that the *p*-values of such tests should in fact lie between this extreme and one in which observations are considered independent (Baayen et al. 2008), we also performed the randomization tests without the nested structure. Differences in mean index values between each cover type were compared to the differences in means obtained from 999 randomizations. Two-sided *p*-values were computed by determining the proportion of absolute differences that were equal to or greater than the observed difference between the two treatments. Analyses were performed with R v. 3.2.3 (R Core Team 2015) and data from both analyses are provided in Appendix 2.

# RESULTS

## Homing time

We performed a total of 60 translocations in the 3 cover types (Table 1). Overall, 38% of translocated individuals homed successfully within 5 h: 6 out of 21 in untreated forest stands, 5 out of 18 in partially harvested forest stands, and 12 out of 21 in conifer plantations (Table 1; Fig. 3). For successful individuals, mean homing time was 157 min. (fastest = 80 min.) in untreated forest, 118 min. (fastest = 74 min.) in partially harvested forest, and 126 min. (fastest = 56 min.) in conifer plantations. There was no evidence for differences in homing time among cover types, as the null model was better supported by the data ($w_i = 0.72$) than the model including cover type ($w_i = 0.28$, $\Delta\_AIC_c = 1.89$, min. $AIC_c = 177.37$; Table 2). Following the 5 hours of monitoring, logistical constraints did not allow for a systematic verification of the fate of the 37 individuals that had not yet returned to their capture site. However, we were able to confirm that 21 of them had returned within 14 days when attempting to retrieve transmitters.

**Table 1**. Number of Ovenbirds (*Seiurus aurocapilla*) translocated over ~500 m in 3 different cover types.

| Cover type[†] | Site | Number of individuals | | Total |
|---|---|---|---|---|
| | | Translocated | Returned within 5h | |
| Untreated | F | 9 | 2 | 21 |
| Untreated | G | 6 | 3 | |
| Untreated | H | 6 | 1 | |
| Conifer plantations | I | 8 | 4 | 21 |
| Conifer plantations | J | 7 | 6 | |
| Conifer plantations | K | 6 | 2 | |
| Partially harvested | L | 6 | 0 | 18 |
| Partially harvested | M | 6 | 4 | |
| Partially harvested | N | 6 | 1 | |

[†] Untreated: untreated mature deciduous stands, Partially harvested: partially harvested deciduous stands, and conifer plantations.

**Fig. 3**. Cumulative proportion of Ovenbirds (*Seiurus aurocapilla*) that returned to their territory and return time following experimental translocations over ~500 m in 3 different types of forest cover in northwestern New Brunswick: partially harvested mature deciduous forest, untreated mature deciduous forest, and ~40-year-old spruce plantation.

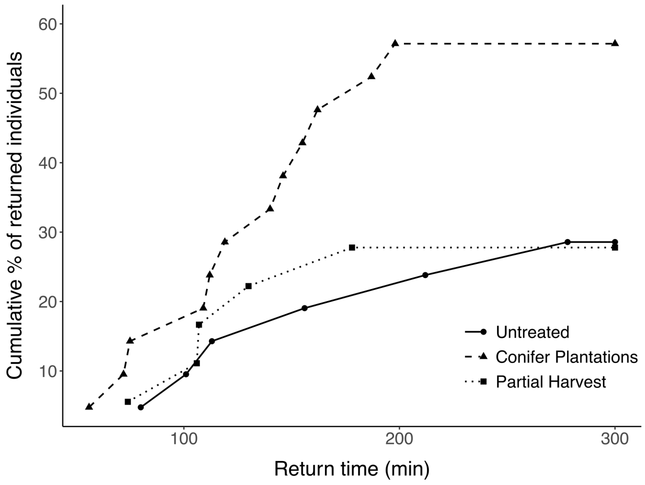


**Table 2**. Parameter estimates and associated SE of Cox mixed regressions used to model the homing time of 60 Ovenbirds (*Seiurus aurocapilla*) translocated over ~500 m in 3 different cover types (see Table 1).

| Parameter[†] | β | SE | 95% Confidence interval | |
|---|---|---|---|---|
| | | | Lower limit | Upper limit |
| Untreated | -0.952 | 0.658 | -2.241 | 0.337 |
| Partially harvested | -0.905 | 0.682 | -2.241 | 0.432 |

[†] Partially harvested: deciduous stands with 5-m wide cut strips; Mature deciduous: untreated mature deciduous stands reflecting breeding habitat. Reference category for cover type was conifer plantations, i.e., ~40 year-old spruce plantations.

## Homing movement patterns

We characterized the movement patterns of 52 individuals (n = 17 for untreated stands, n = 17 for conifer plantations, n = 18 for partial harvest) based on the geographical locations taken along their homing path. Out of six possible combinations of forest-cover types and indices, two suggested differences among cover types (Fig. 4; Appendix 1, A1.11). First, there was a tendency for birds released in conifer plantations to follow a straighter path compared to those released in untreated stands (IST: 1.83 vs. 3.74, $0.04 \leq p \leq 0.06$; Fig. 4b; Appendix 1, A1.11b; Table 3). Second, birds released in conifer plantations also tended to travel faster than those released in untreated stands (global speed: 4.27 m/min vs. 1.90 m/min, $0.02 \leq p \leq 0.11$; Fig. 4e, Appendix 1, A1.11e; Table 3). Mean IST values were 1.51 (range: 1.00-2.44) and 3.60 (range: 1.04-17.02) for birds that returned or not within five hours, respectively (Fig. 5). Returning birds also showed a mean global speed of 5.73 m/min (range: 2.46-14.82 m/min), compared to 1.28 m/min (range: 0.25-3.01 m/min) for those that did not (Fig. 6). The correlation (Kendall's tau) between IST and global speed was -0.16, suggesting a low negative association between these two movement components.

**Table 3**. Mean value and associated coefficient of variation (CV in %) of two indices used to characterize the homing patterns of 60 Ovenbirds (*Seiurus aurocapilla*) translocated over ~500 m in 3 different cover types (see Table 1).

| | IST[†] | | Global speed (m/min) | |
|---|---|---|---|---|
| Cover type | Mean | CV | Mean | CV |
| Untreated | 3.74 | 107.7 | 1.90 | 85.0 |
| Conifer plantations | 1.83 | 41.6 | 4.27 | 81.2 |
| Partial harvest | 2.91 | 94.6 | 2.58 | 88.4 |

[†] IST: Inverse straightness index is defined as the total length of the path followed by the individual $L$ divided by the Euclidean distance between the release and capture sites (d). The closer the IST is to 1, the straighter the path is, with greater values indicating higher levels of tortuosity.

# DISCUSSION

Individuals showed coherent trends indicating that movement differed within conifer plantations compared to untreated stands. Individuals released within conifer plantations tended to follow

**Fig. 4**. Results of hierarchical randomization tests for two movement behavior indices, inverse straightness index (IST) and global speed (m/min), for Ovenbirds (*Seiurus aurocapilla*) translocated over ~500 m in 3 cover types. Differences in mean index values between each cover type (shown by vertical dotted lines) were compared to the differences in randomly generated means. The two-tailed p-value is shown above the histograms. The cover types are Partial. Harvest.: deciduous forest with 5-m wide cut strips; Untreat. Dec.: untreated mature deciduous forest (typical breeding habitat); Conifer Plant.: ~40-year-old spruce plantation.

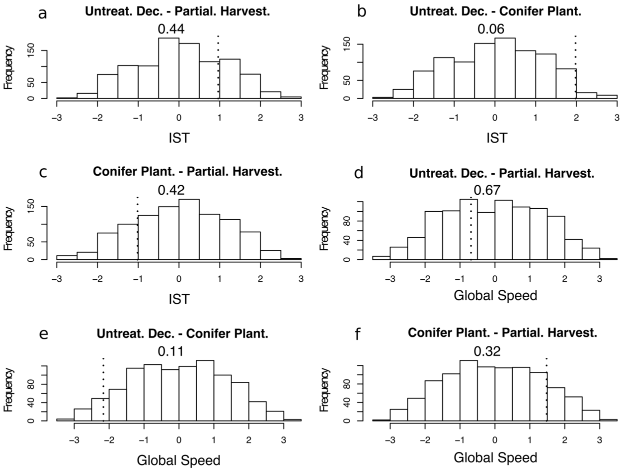


**Fig. 5**. Density curves showing the distribution of values for the inverse straightness index (IST) for returned (1) and non-returned (0) individuals translocated over 500 m in 3 cover types (partially harvested, deciduous forest with 5-m wide cut strips; untreated mature deciduous forest; ~40-year-old spruce plantations). Homing was considered successful when an individual arrived within 50 m from its capture site, when released in untreated forest, or when it reached the untreated forest edge, when released in one of the other forest-cover types. The dashed lines represent mean IST values for each category. Values closer to 1 indicate straighter movement paths.

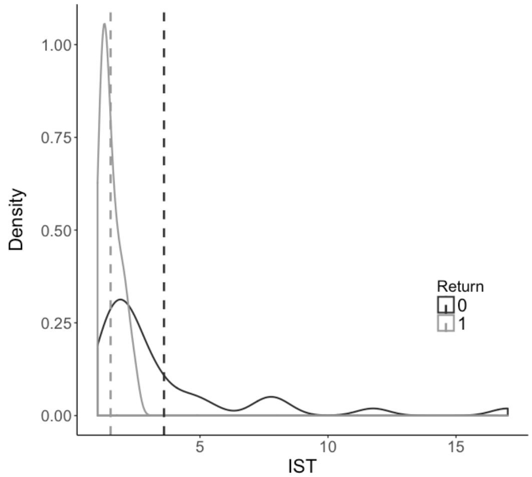
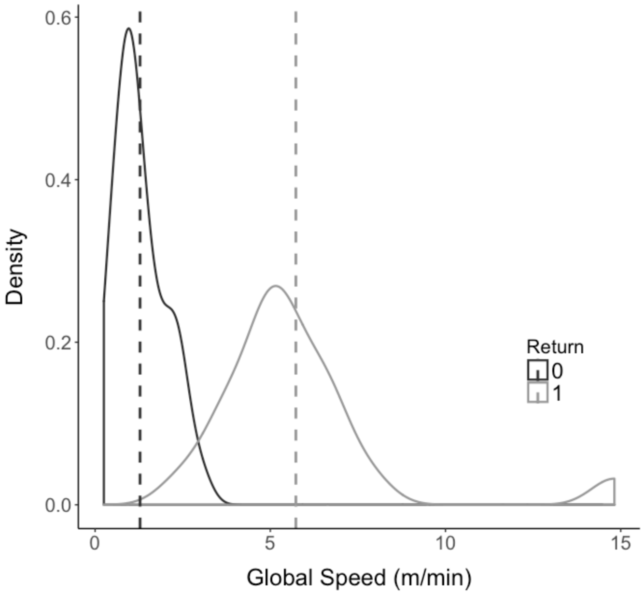


**Fig. 6**. Density curves showing the distribution of values for the global traveling speed (m/min) for returned (1) and non-returned (0) individuals translocated over 500 m in 3 cover types (partially harvested, deciduous forest with 5-m wide cut strips; untreated mature deciduous forest; ~40-year-old spruce plantations). Homing was considered successful when an individual arrived within 50 m from its capture site, when released in untreated forest, or when it reached the untreated forest edge, when released in one of the other forest-cover types. The dashed lines represent the mean speed value for each category.



a straighter path and to move faster than those released within untreated deciduous stands. When comparing distributions of path tortuosity index values between individuals that returned or not within five hours independently of cover type, successful individuals appeared to follow straighter paths and to travel faster than those that did not return. Considering that a higher proportion of individuals returned when released within conifer plantations, it is not surprising that they also tended to follow straighter paths and maintain faster travel speeds. Moreover, even though tortuosity and speed were likely negatively correlated, which could explain why fast individuals also seemed to have straighter paths, the suspected effect of forest-cover type on movement pattern still remains.

The movement patterns we observed were consistent with our prediction that individuals released within conifer plantations would exhibit behaviors increasing the likelihood of exiting inhospitable land cover (Van Dyck and Baguette 2005, Brown et al. 2017). Also, as predicted, individuals released within untreated stands exhibited movements typical of searching and foraging behaviors (Van Dyck and Baguette 2005, Barraquand and Benhamou 2008). This behavioral pattern, in which high-quality habitat is associated with slow and sinuous movements whereas poor-quality habitat is associated with fast and straight movements, has been reported in multiple taxa including goldenrod beetles (*Trirhabda borealis*; Goodwin and Fahrig 2002), butterflies (Delattre et al. 2010, Brown et al. 2017), hedgehogs (*Erinaceus europaeus*; Doncaster et al. 2001), and woodland caribou (*Rangifer tarandus caribou*; Johnson et al. 2002). This phenomenon is likely attributable to the travel costs and benefits associated with each cover type. For instance, inhospitable land-cover types (which often form the “matrix”) are generally characterized by lower food availability, higher predation risk, and sometimes lower perceptual range; the latter being associated with a higher mortality risk and lower efficiency while searching for nearby habitat (Baguette et al. 2012 and references therein). If we assume that dispersing individuals attempt to minimize movement costs (Baguette et al. 2012), then they should avoid crossing edges separating habitat from inhospitable land-cover types. It follows that when inhospitable land-cover types cannot be avoided, or when individuals decide to cross them (e.g., to avoid long detours), they should move as efficiently as possible. Faster and straighter travel paths would therefore be expected to reflect higher travel costs induced by the land covers being crossed.

Our experiment suggests that not all forest-cover types were equal with respect to their resistance to Ovenbird movements, and likely to those of other forest songbirds exhibiting similar levels of habitat specialization or reluctance to cross non-forested areas. Although we only found coherent trends indicative of this phenomenon, potentially due to low statistical power, we believe that this finding may have major implications for the assessment of functional connectivity. It therefore deserves further attention and should be empirically tested with other forest species. This appears especially important when considering that the influence of landscape structure on forest bird movement has generally been assessed by considering forest cover as homogeneous because it contrasted sharply with matrix types such as cropfields, clearcuts, or shrubland (e.g., Bélisle et al. 2001, Gobeil and Villard 2002, Hadley and Betts 2009, Valente et al. 2019).

Because our experiment focused on movement patterns within homogeneous cover types, we cannot report on the crucial step of edge crossing (see also St-Louis et al. 2014). Indeed, forest birds have been shown to spend considerable time facing sharp edges and then to display fast and straight movements across open areas, or simply to avoid crossing open land by taking a detour if the latter is available and not too long in both relative and absolute terms (Desrochers and Hannon 1997, St. Clair et al. 1998, Desrochers and Fortin 2000, Bélisle and Desrochers 2002). That forest birds may move efficiently (i.e., directionally and fast) once they have entered an inhospitable land cover, as observed in this study, is consistent with the quadratic relationship between homing time and amount of habitat reported by Bélisle et al. (2001): although the homing success of translocated forest passerines, including some Ovenbirds, decreased monotonically with forest-cover loss in agricultural landscapes; birds that did home successfully in highly fragmented landscapes did so rapidly. Similarly, Cornelius et al. (2017) reported that the propensity of White-shouldered Fire-eyes (*Piriglena leucoptera*) to cross edges varied as a function of habitat fragmentation in their original landscape: individuals captured in more fragmented landscapes were more reluctant to cross edges following their translocation, but more successful at crossing the matrix. Our results are consistent with the notion that landscape functional connectivity is a cumulative function of both within- and between-habitat (edge) movement responses (Bélisle 2005).

That being said, very few studies have investigated edge effects among weakly contrasting cover types, such as the different forest stand types considered here. Knowlton et al. (2017) documented the movements of Cinereous Antshrikes (*Thamnomanes caesius*) translocated across forest landscapes comprising large patches of oil palm plantations. The majority of individuals took longer routes to avoid traveling across plantations and routine movements of non-translocated birds holding territories < 200 m from the edge of an oil palm plantation never occurred within the plantation itself. Given that bird response to edges is known to vary with their nature and sharpness (Ries et al. 2004, Stevens et al. 2006, Reino et al. 2009), it may be necessary to qualify edge sharpness according to plant species composition in addition to vegetation structure (e.g. St-Louis et al. 2004) to derive resistance values specific to each type of edge when estimating functional connectivity.

As part of our experiment, we had to make compromises among translocation distances, recording frequency of a focal individual's location, precision of homing time estimation, and sample size (number of translocations performed). We reasoned that 500 m would be far enough for the birds to exhibit variation in their behavior, while allowing us to actively track their homing path within a reasonable amount of time. Moreover, movement behavior indices such as IST are known to yield more realistic values when locations are recorded at a high frequency (Benhamou 2004), which is easier to do with short translocation distances. However, movement behaviors exhibited by individuals homing over 500 m may not be representative of dispersing individuals. Songbirds can perform off-territory exploratory movements (e.g., up to 2.5 km in Hooded Warbler, *Setophaga citrina*; Norris and Stutchbury 2001). Hence, birds translocated 500 m away from their territory may not encounter fully novel conditions, contrary to dispersing juveniles. However, dispersal may not only result from directed, fast, and long-distance movements away from natal or previous breeding sites, but also from routine movements related to daily activities (Van Dyck and Baguette 2005). Volpe et al. (2014) found that Green Hermits (*Phaethornis guy*) translocated over 340-1500 m displayed movement behaviors similar to those of individuals performing routine movements. Therefore, the movement behaviors documented during our translocation experiment may accurately reflect the Ovenbird's perception of the traveling costs associated with the different forest-cover types we considered, and hence the propensity to move across a relatively familiar landscape.

A high proportion (62%) of birds had not yet returned to their capture sites five hours after their release. Owing to logistical constraints and trade-offs in survey effort, we could not monitor homing individuals for more than five hours, neither could we systematically confirm the fate of non-returned individuals. However, it seems that five hours was simply not enough time for them to return. Indeed, we confirmed the presence at the capture site of at least 57% of the non-returned individuals within 14 days of the translocation. We suspect that non-returned birds may have spent more time foraging than returned birds, as suggested by higher IST values (Appendix 1, Table A1.8, Fig. A1.12; Fig. 5) and lower global speed (Appendix 1, Table A1.8, Fig. A1.13; Fig. 6; Van Dyck and Baguette 2005, Barraquand and Benhamou 2008) and because birds were almost always observed on the ground when not in movement. This pattern could potentially indicate that the birds were trying to recover from handling stress. Even though we did not include handling time in our models, an effect of handling stress on homing would be expected to be similar among cover types. Indeed, treatments were allocated haphazardly among birds and the distributions of handling times were similar among cover types (Appendix 1, Fig. A1.9). It is also possible that some individuals may have established new territories near their translocation site when released in untreated forest, as reported by Villard and Haché (2012), although birds were translocated over much longer distances in the latter case. Hence, we believe that it would be the exception more than the rule, especially knowing that our birds were translocated only over 500 m and that wood-warblers are known to perform extra-territorial forays of up to 2.5 km (Norris and Stutchbury 2001).

## CONCLUSION

We reported a set of coherent trends indicating that homing patterns differed between translocated individuals released within conifer plantations and untreated, mature deciduous forest stands. Our results further suggest that edge-crossing decisions can have an influence on homing patterns, even under forest cover. If decision making by traveling individuals mainly takes place at edges, then future studies should compare behavioral responses among various types of edges, including ecotones between forest-cover types. Addressing this can be very challenging or even impossible for small vagile organisms with current tracking technologies. However, homing and gap-crossing experiments designed to impose multiple edge-crossings while standardizing individual motivation represent promising complementary approaches. Such empirical work is essential to derive realistic landscape resistance values to estimate landscape functional connectivity and, ultimately, to model population dynamics.

*Responses to this article can be read online at:*
https://www.ace-eco.org/issues/responses.php/1831

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# Appendix #1

Functional connectivity of managed forest landscapes for the Ovenbird: an experimental assessment of within-patch movement behavior – *Avian Conservation and Ecology, 2021*

CATHERINE GEOFFROY, MARC-ANDRÉ VILLARD and MARC BÉLISLE

**Table A1.1**: Mean value and associated coefficient of variation (CV in %) of two indices used to characterize the homing patterns of 60 Ovenbirds translocated over ~500 m in three different cover types (see Table 1) for returned and non-returned individuals. Homing was considered successful when an individual arrived within 50 m from its capture site, when released in untreated forest, or when it reached the untreated forest edge, when released in one of the other forest cover types.

| | IST[†] | | Global speed (m/min) | |
|---|---|---|---|---|
| Cover Type | Mean | CV | Mean | CV |
| Returned - Untreated | 1.40 | 28.8 | 4.08 | 43.2 |
| Returned - Conifer plantations | 1.58 | 21.8 | 6.28 | 50.6 |
| Returned - Partial harvest | 1.45 | 39.0 | 5.94 | 15.7 |
| Non-returned - Untreated | 4.47 | 98.2 | 1.23 | 64.6 |
| Non-returned - Conifer plantations | 2.19 | 48.1 | 1.38 | 44.7 |
| Non-returned - Partial harvest | 3.47 | 88.4 | 1.28 | 56.5 |

[†] IST : Inverse straightness index is defined as the total length of the path followed by the individual *L* divided by the Euclidean distance between the release and capture sites (d). The closer the IST is to 1, the straighter the path is, with greater values indicating higher levels of tortuosity.

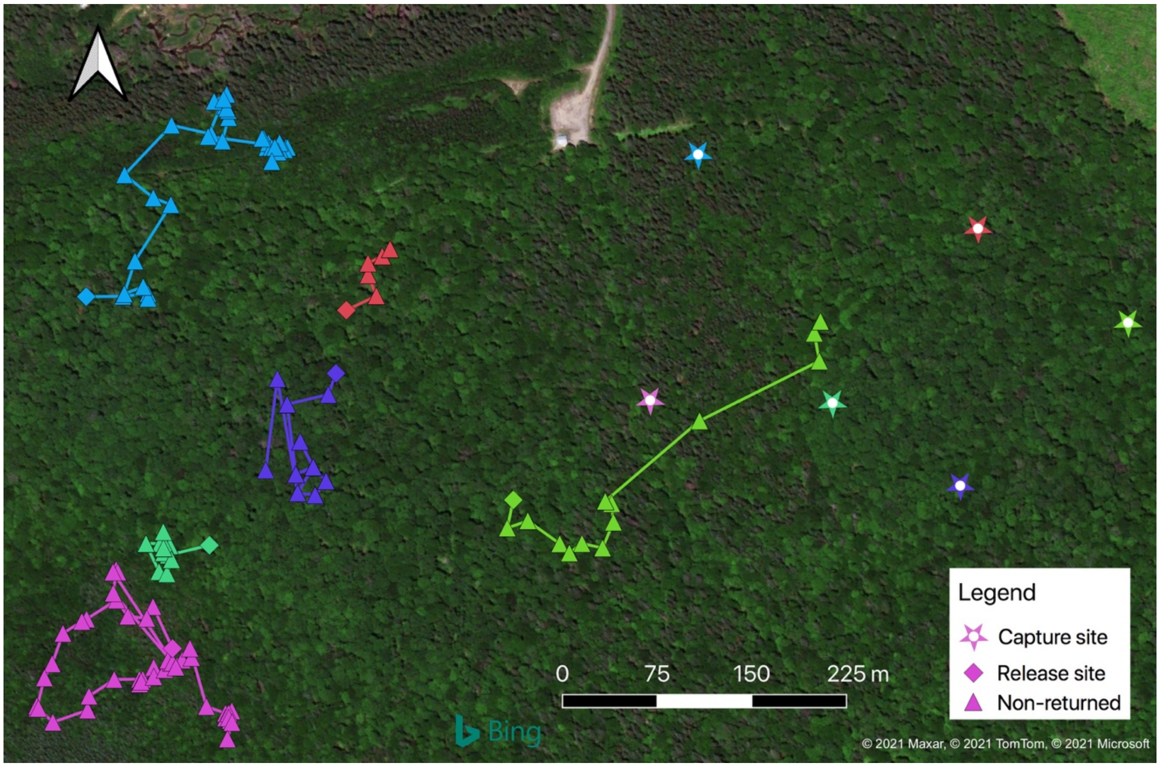

**Fig. A1.1** Paths taken by Ovenbird individuals following experimental translocation over ~500 m in untreated mature deciduous forest (site 2). Homing was considered successful when an individual arrived within 50 m from its capture site.

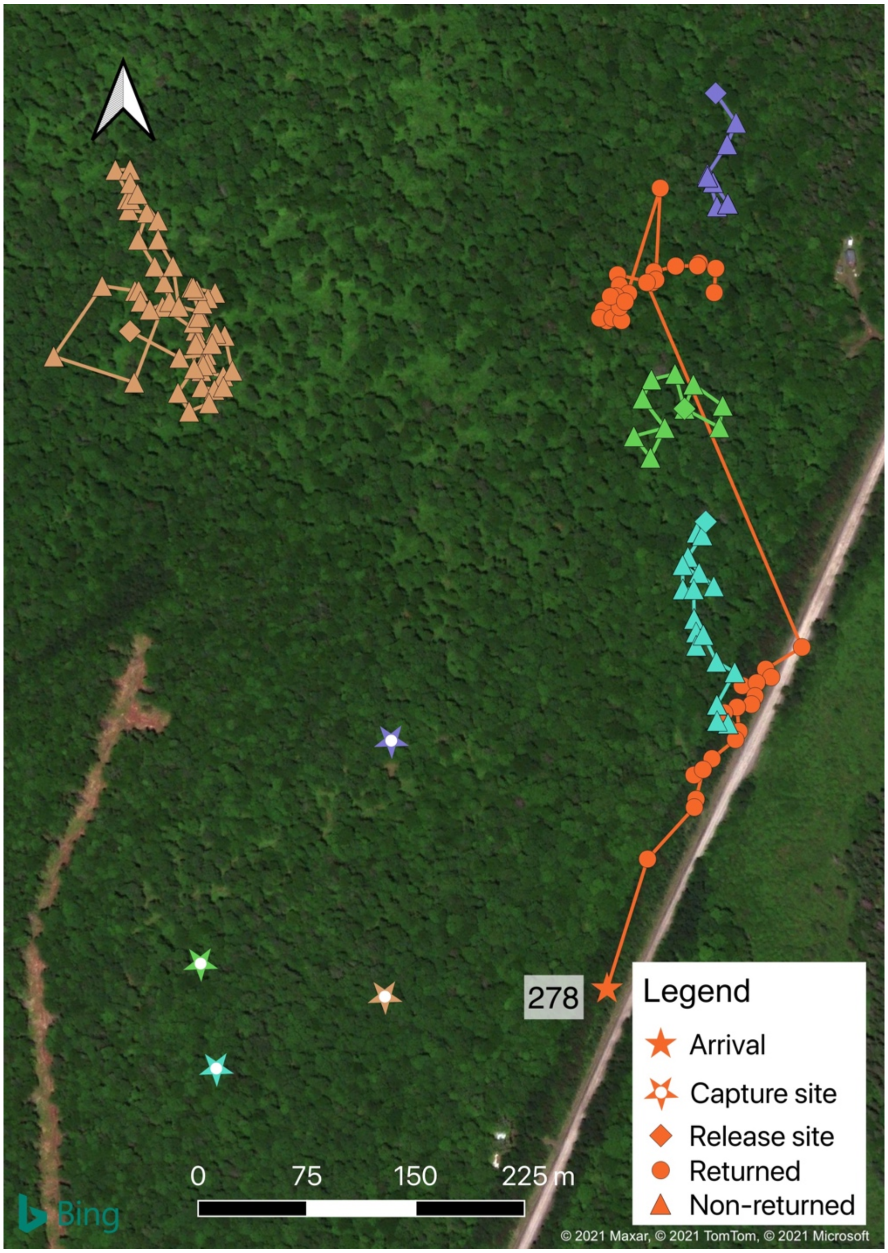

**Fig. A1.2** Paths taken by Ovenbird individuals following experimental translocation over ~500 m in untreated mature deciduous forest (site 3). Release sites are shown only for non-returned individuals to indicate movement direction. Capture sites are shown if different from arrival and for non-returned individuals. Return time (min) is shown next to arrival. Homing was considered successful when an individual arrived within 50 m from its capture site.

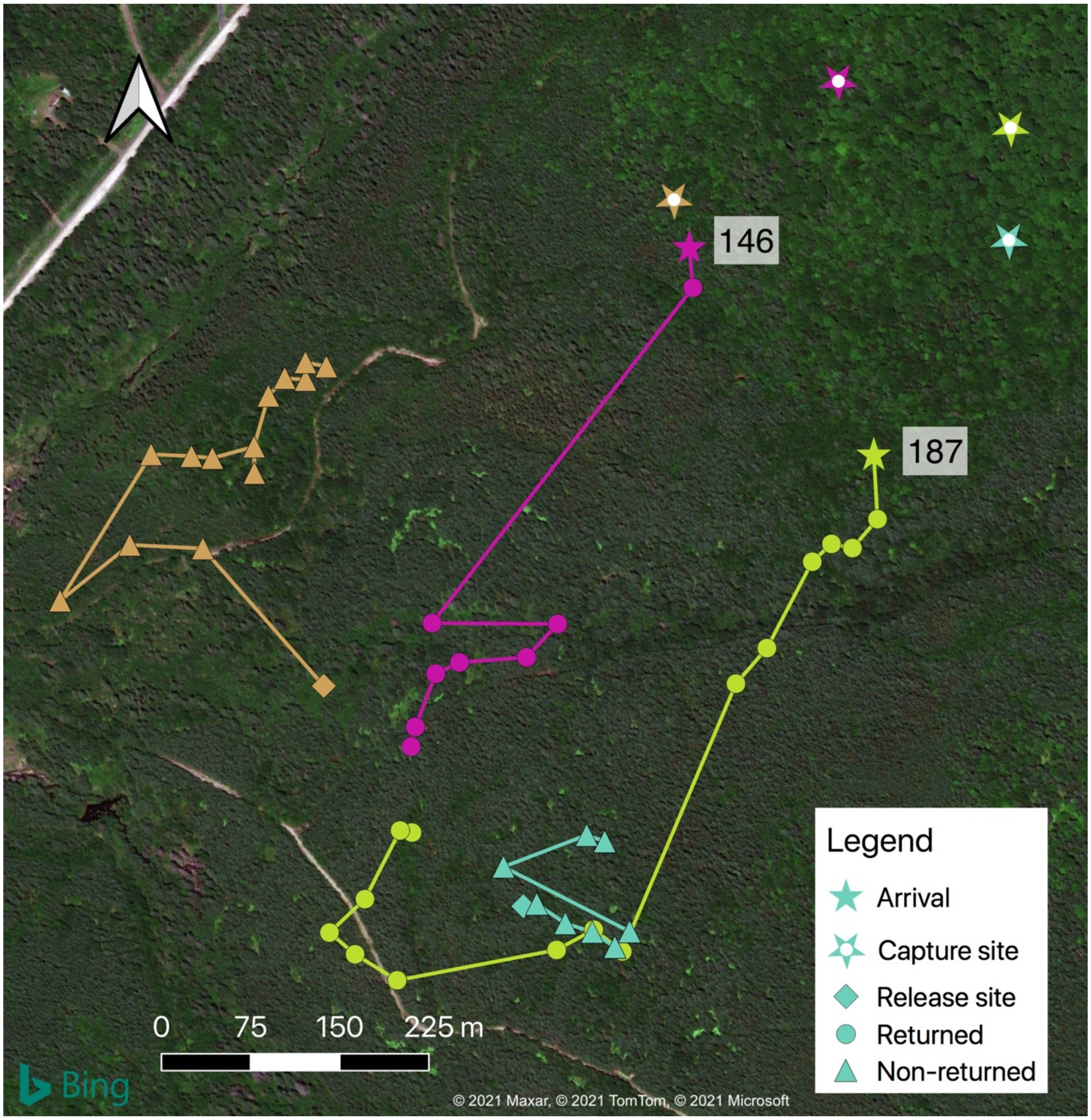

**Fig. A1.3** Paths taken by translocated Ovenbirds captured in untreated mature deciduous forest and released ~500 m away in conifer plantation (site 2). Release sites are shown only for non-returned individuals to indicate movement direction. Capture sites are shown if different from arrival and for non-returned individuals. Return times (min) are shown next to arrival. Homing was considered successful when individuals reached the untreated forest edge.

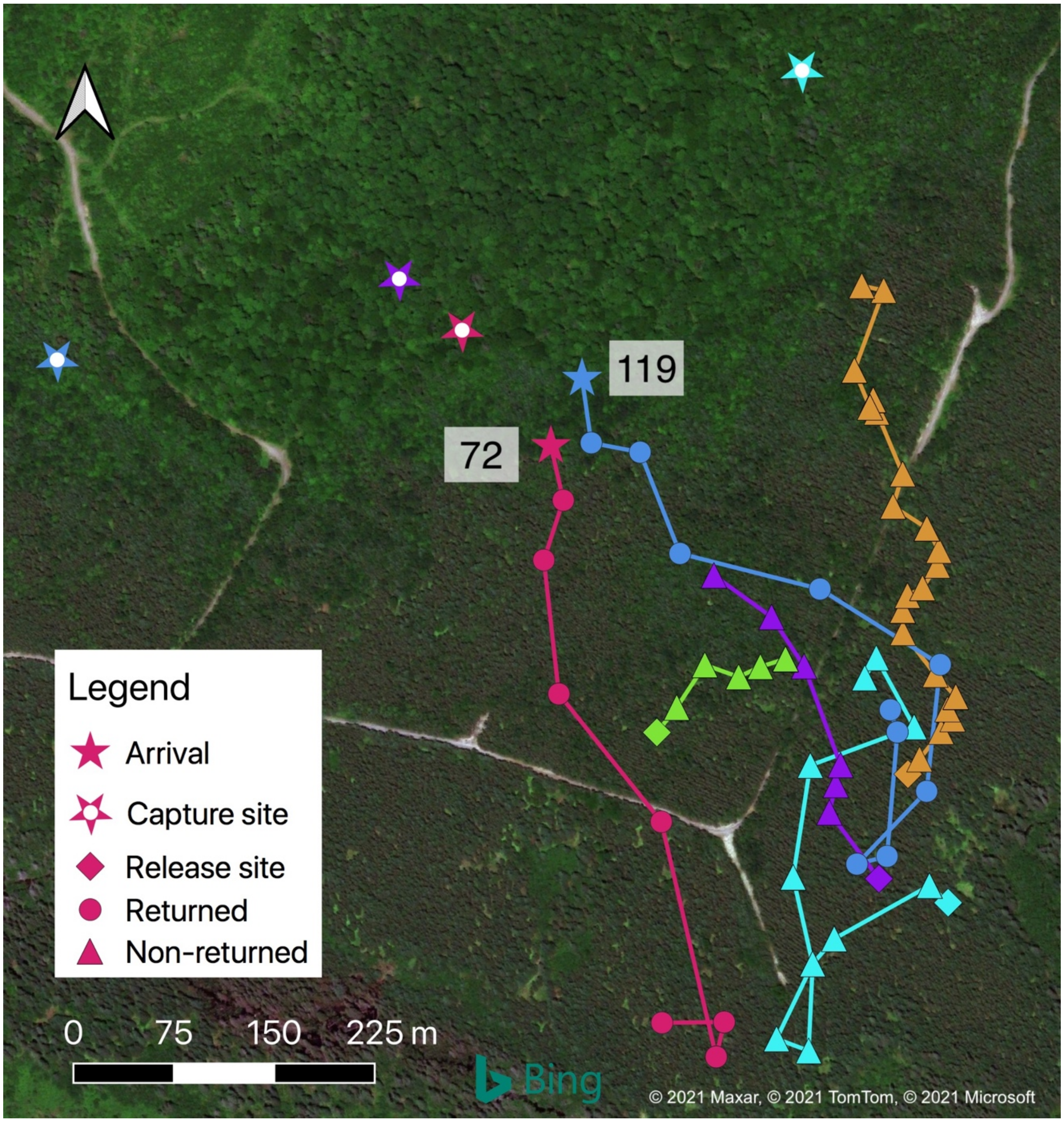

**Fig. A1.4** Paths taken by translocated Ovenbirds captured in untreated mature deciduous forest and released ~500 m away in conifer plantation (site 3). Release sites are shown only for non-returned individuals to indicate movement direction. Capture sites are shown if different from arrival and for non-returned individuals. Return times (min) are shown next to arrival. Homing was considered successful when individuals reached the untreated forest edge.

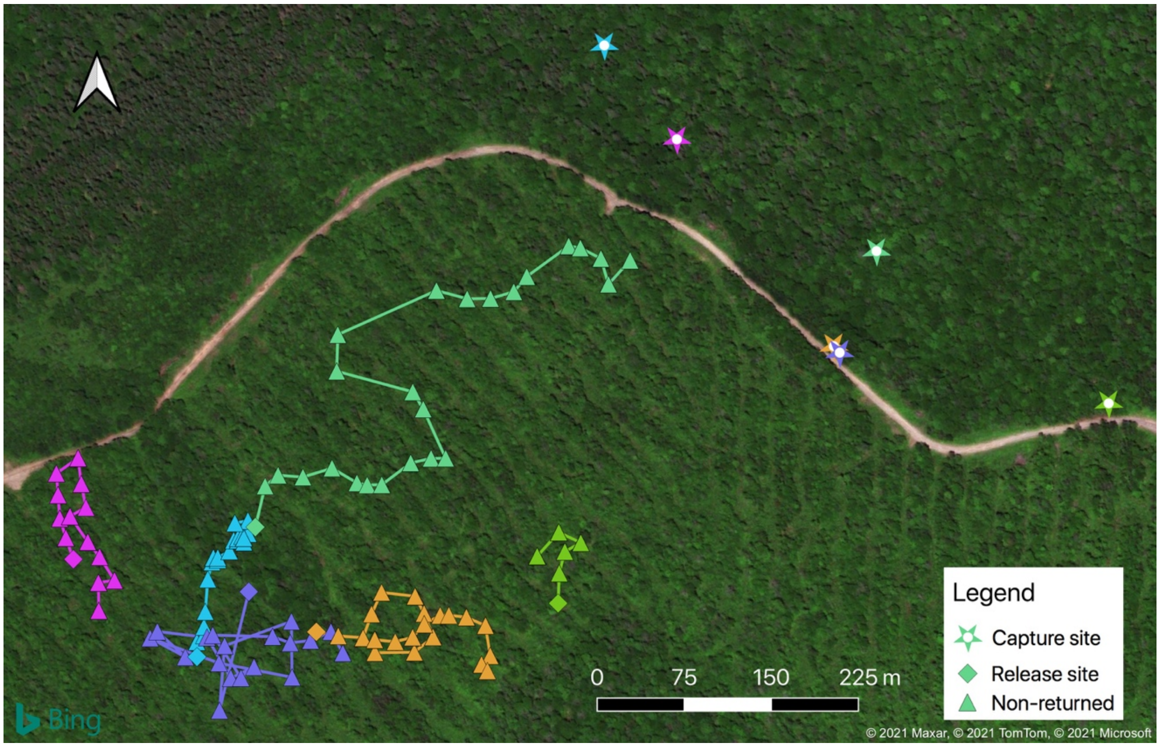

**Fig. A1.5** Paths taken by translocated Ovenbirds captured in untreated mature deciduous forest and released ~500 m away in partially harvested mature deciduous forest (site 1). Homing was considered successful when individuals reached the untreated forest edge.

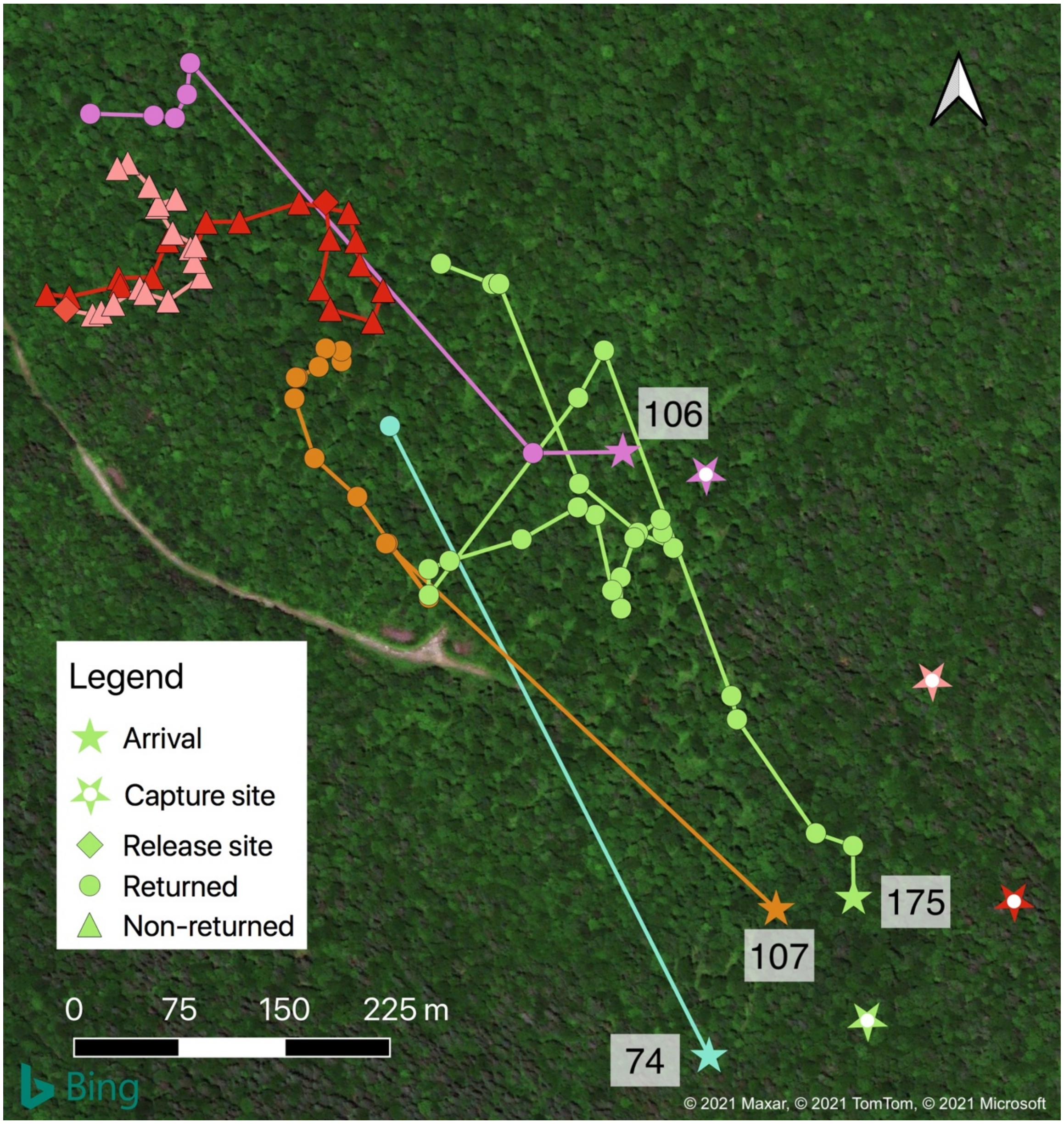

**Fig. A1.6** Paths taken by translocated Ovenbirds captured in untreated mature deciduous forest and released ~500 m away in partially harvested mature deciduous forest (site 2). Release sites are shown only for non-returned individuals to indicate movement direction. Capture sites are shown if different from arrival and for non-returned individuals. Return times (min) are shown next to arrival. Homing was considered successful when individuals reached the untreated forest edge.

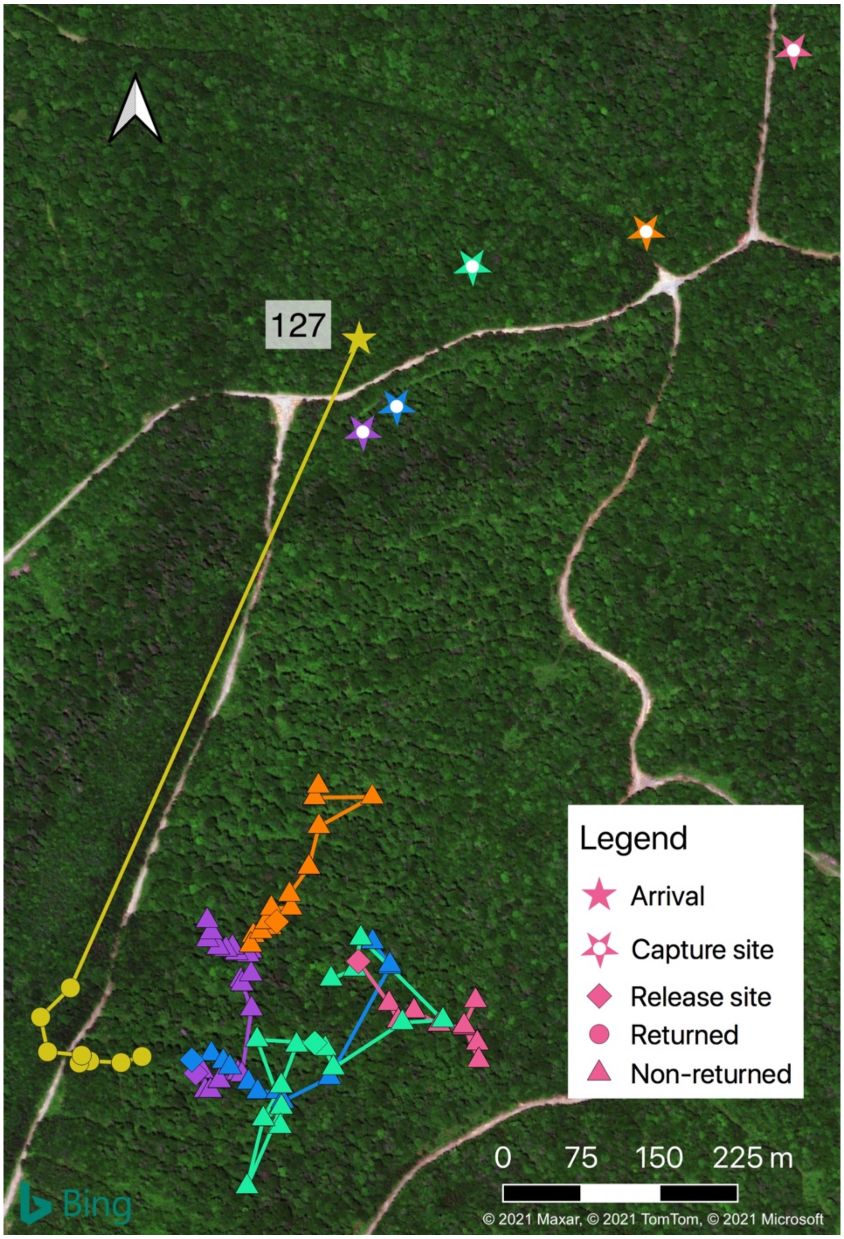

**Fig. A1.7** Paths taken by translocated Ovenbirds captured in untreated mature deciduous forest and released ~500 m away in partially harvested mature deciduous forest (site 2). Release sites are shown only for non-returned individuals to indicate movement direction. Capture sites are shown if different from arrival and for non-returned individuals. Return time (min) is shown next to arrival. Homing was considered successful when individuals reached the untreated forest edge.

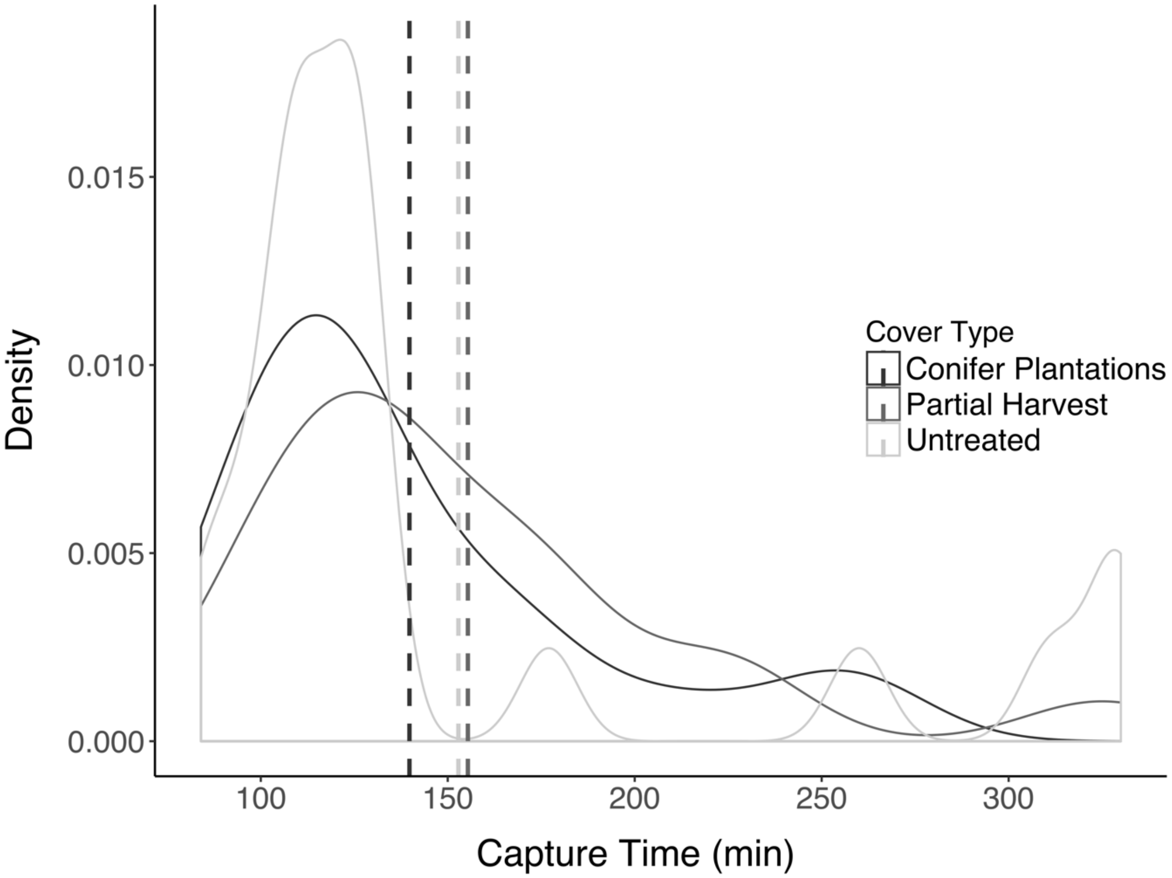

**Fig. A1.8** Density curves showing the distribution of values for the time of capture relative to sunrise for individuals translocated over 500 m in 3 cover types (partially-harvested, deciduous forest with 5-m wide cut strips; untreated mature deciduous forest; ~40-year-old spruce plantation). The dashed lines represent the mean speed value for each category.

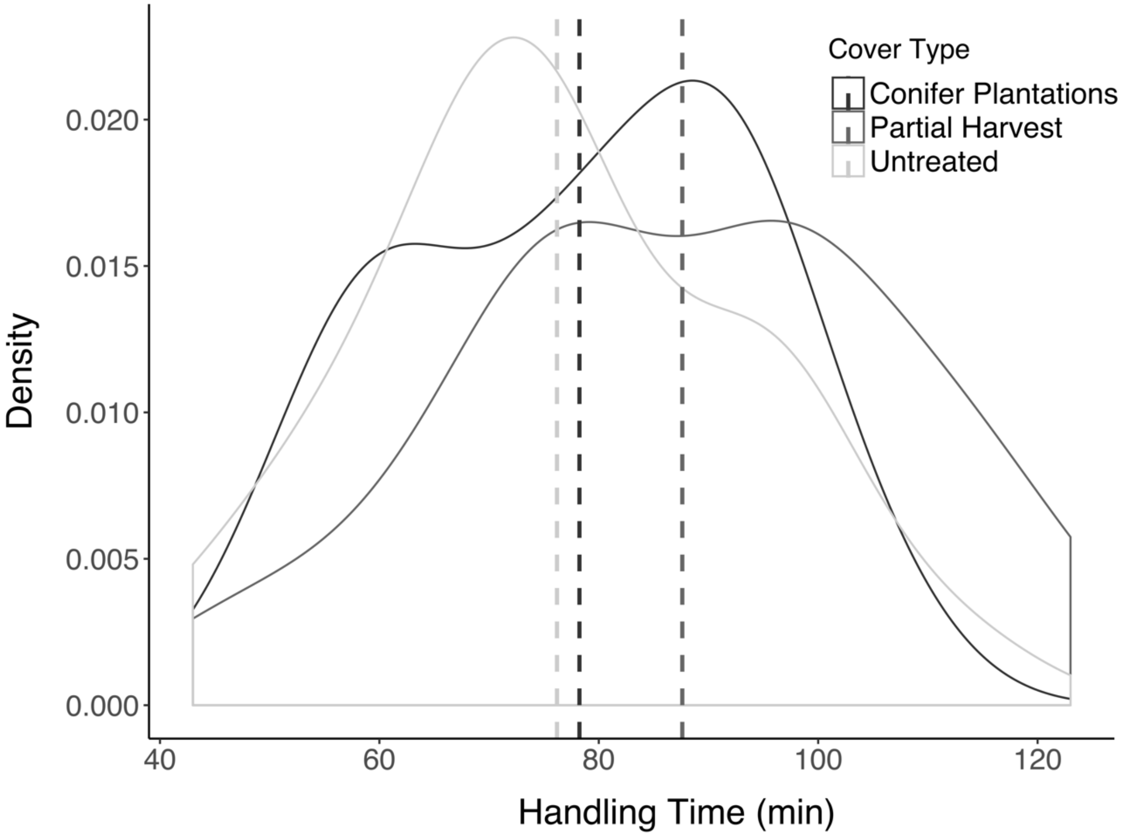

**Fig. A1.9** Density curves showing the distribution of values for the time elapsed between capture and release for individuals translocated over 500 m in 3 cover types (partially-harvested, deciduous forest with 5-m wide cut strips; untreated mature deciduous forest; ~40-year-old spruce plantation). The dashed lines represent the mean speed value for each category.

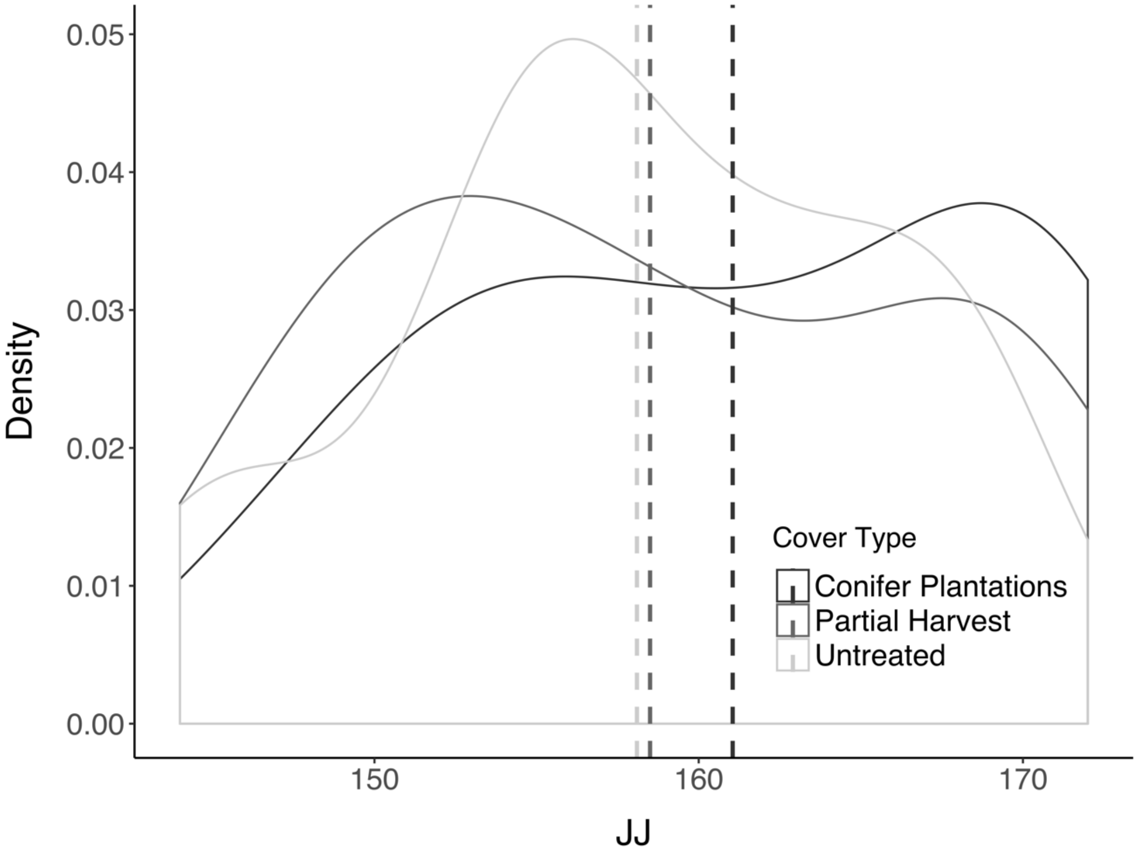

**Fig. A1.10** Density curves showing the distribution of values for Julian day of translocation for individuals translocated over 500 m in 3 cover types (partially-harvested, deciduous forest with 5-m wide cut strips; untreated mature deciduous forest; ~40-year-old spruce plantation). The dashed lines represent the mean speed value for each category.

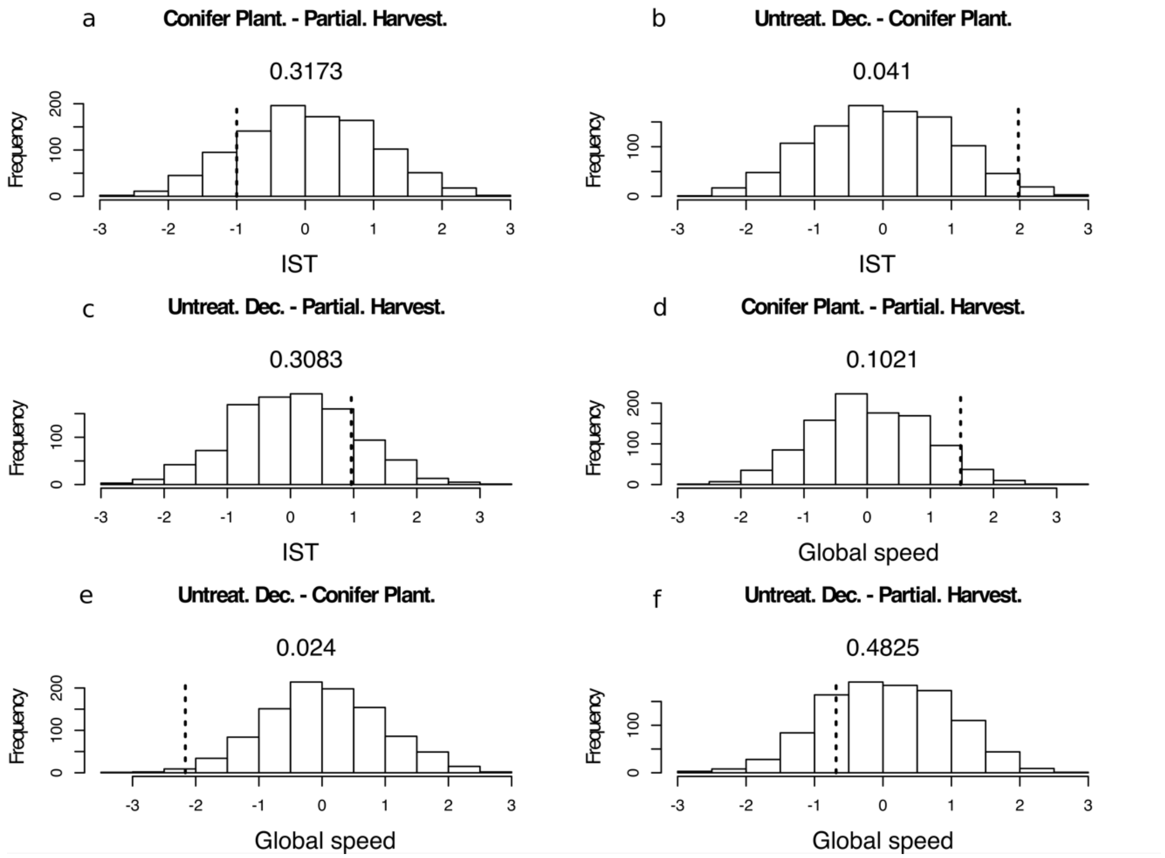

**Fig. A1.11** Results of randomization tests assuming that the observations were not nested within sites, and this for two movement behavior indices, inverse straightness index (IST) and global speed, for Ovenbirds translocated over ~500 m in three cover types. Differences in mean index values between each cover type (shown by vertical dotted lines) were compared to the differences in randomly generated means. The two-tailed *p*-value is shown above the histograms. The cover types are Partial. Harvest.: deciduous forest with 5-m wide cut strips; Untreat. Dec.: untreated mature deciduous forest (typical breeding habitat); Conifer Plant.: ~40-year-old spruce plantation.

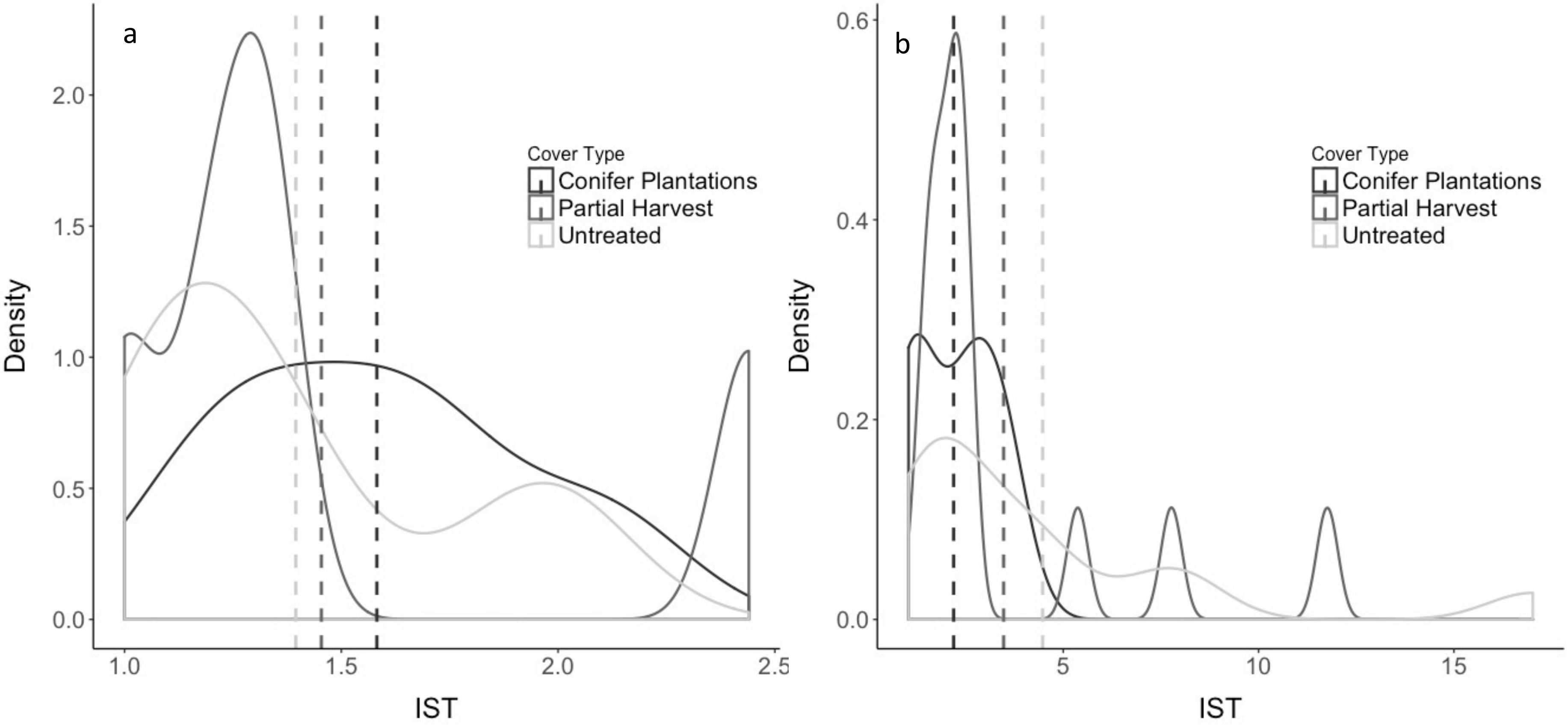

**Fig. A1.12** Density curves showing the distribution of values for the inverse straightness index (IST) for returned (a) and non-returned (b) individuals translocated over 500 m in three cover types (partially-harvested, deciduous forest with 5-m wide cut strips; untreated mature deciduous forest; ~40-year-old spruce plantation). The dashed lines represent mean IST values for each category. Values closer to 1 indicate straighter movement paths.

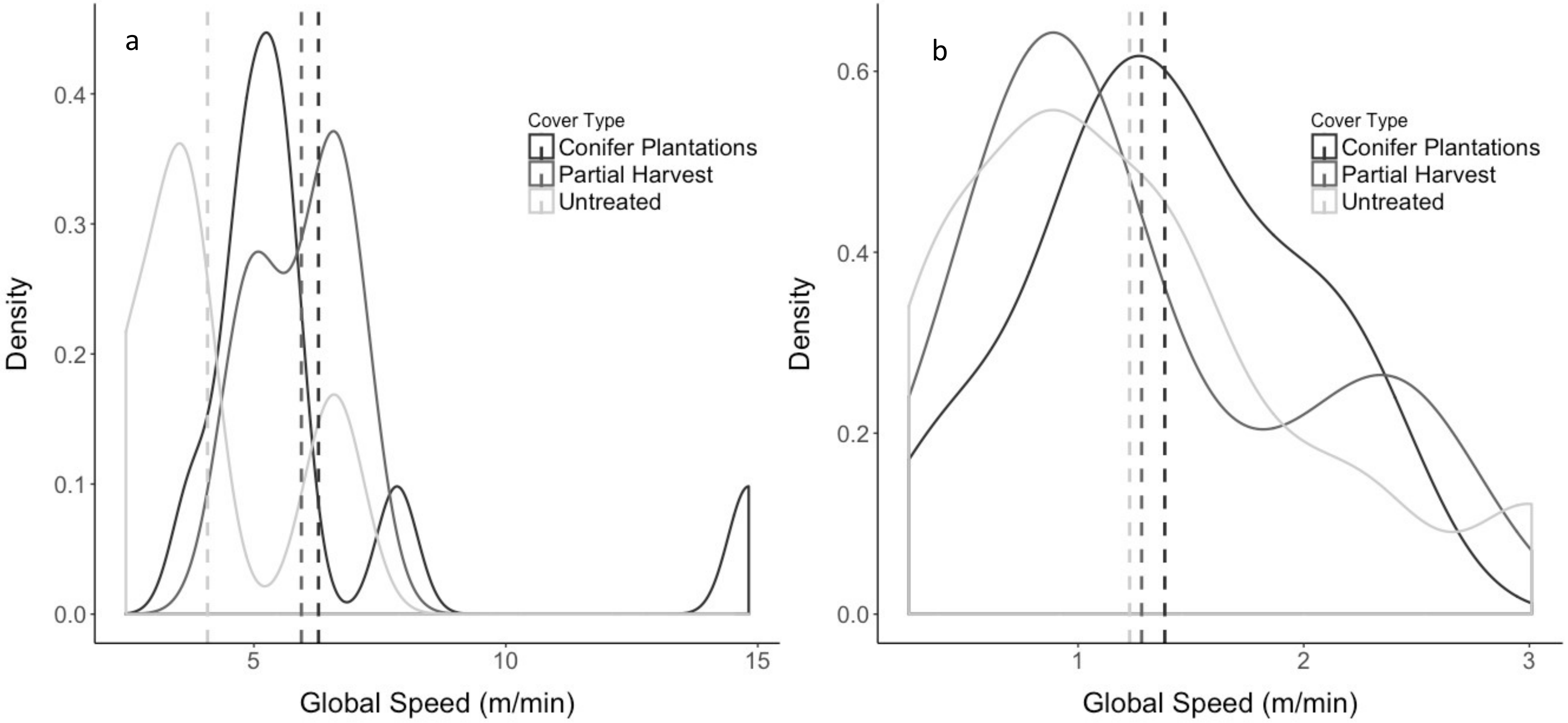

**Fig. A1.13** Density curves showing the distribution of values for the global travelling speed (m/min) for returned (a) and non-returned (b) individuals translocated over 500 m in 3 cover types (partially-harvested, deciduous forest with 5-m wide cut strips; untreated mature deciduous forest; ~40-year-old spruce plantation). The dashed lines represent the mean speed value for each category.

## Appendix #2

Functional connectivity of managed forest landscapes for the Ovenbird: an experimental assessment of within-patch movement behavior – *Avian Conservation and Ecology, 2021*

CATHERINE GEOFFROY, MARC-ANDRÉ VILLARD and MARC BÉLISLE

Table A.2.1 Description of the data presented in Table A2.2

| Variable | Description |
|---|---|
| Cover Type | Forest-cover type of release areas; untreated mature deciduous forest stands, partially-harvested deciduous forest stands and conifer plantations |
| Site | Release area, three per cover type |
| Julian Day (Jul_Day) | Day of translocation |
| Time of Capture (Capt_Time) | Time elapsed between sunrise and capture of the individual (min) |
| ID | Bird ID |
| Observer (Obs) | Observer who performed the monitoring of the homing |
| Time of release (Rel_Time) | Time elapsed between sunrise and release of the individual (min) |
| Return Time | Time elapsed between release and arrival within 50 m from its capture site, when released in untreated forest, or when it reached the untreated forest edge, when released in one of the other forest-cover types. Unsuccessful individuals were assigned 300 (min) |
| Return | Whether or not the individual returned to its capture site within 5 hours (1:yes, 0:no) |
| Handling Time (Handl_Time) | Time elapsed between capture and release (min) |
| IST | Inverse Straightness Index; total length of the path followed by the individual *L* divided by the Euclidean distance between the release and capture sites (d) |
| Global Speed (Glob_Speed) | Total path length *L* divided by the total time elapsed between release and arrival, or 5 hours if the individual did not return to the capture site (m/min) |

Table A.2.2 Data used to compute the Cox regression models and randomization tests to characterize homing movement patterns.

| Site | Cover_Type | Jul_Day | Capt_time | ID | Obs | Rel_time | Return_Time | Return | Handl_time | IST | Glob_Speed |
|---|---|---|---|---|---|---|---|---|---|---|---|
| F | Untreated | 144 | 108 | 1 | 5 | 187 | 300 | 0 | 79 | 8.19 | 2.29 |
| F | Untreated | 169 | 260 | 2 | 5 | 314 | 300 | 0 | 54 | 1.39 | 1.31 |
| F | Untreated | 169 | 98 | 3 | 6 | 193 | 300 | 0 | 95 | 1.23 | 0.25 |
| F | Untreated | 157 | 127 | 4 | 5 | 199 | 300 | 0 | 72 | 3.45 | 0.44 |
| F | Untreated | 157 | 311 | 5 | 4 | 390 | 300 | 0 | 79 | 4.52 | 1.43 |
| F | Untreated | 157 | 84 | 6 | 6 | 162 | 300 | 0 | 78 | 3.07 | 1.86 |
| G | Untreated | 153 | 127 | 7 | 5 | 196 | 113 | 1 | 69 | 1.37 | 6.59 |
| G | Untreated | 167 | 129 | 8 | 3 | 199 | 300 | 0 | 70 | 1.49 | 0.93 |
| G | Untreated | 153 | 106 | 9 | 4 | 199 | 300 | 0 | 93 | 4.62 | 0.8 |
| G | Untreated | 153 | 328 | 10 | 5 | 381 | 156 | 1 | 53 | 1.16 | 3.72 |
| G | Untreated | 167 | 126 | 11 | 5 | 223 | 300 | 0 | 97 | 1.97 | 1.44 |
| G | Untreated | 167 | 90 | 12 | 4 | 154 | 212 | 1 | 64 | 1.08 | 2.46 |
| H | Untreated | 162 | 119 | 13 | 6 | 216 | 300 | 0 | 97 | 2.05 | 0.40 |
| H | Untreated | 162 | 114 | 14 | 5 | 191 | 300 | 0 | 77 | 1.75 | 0.8 |
| H | Untreated | 146 | 177 | 15 | 5 | 251 | 278 | 1 | 74 | 1.97 | 3.55 |
| H | Untreated | 162 | 122 | 16 | 4 | 193 | 300 | 0 | 71 | 7.39 | 1.01 |
| H | Untreated | 162 | 109 | 17 | 3 | 221 | 300 | 0 | 112 | NA | NA |
| H | Untreated | 146 | 111 | 18 | 6 | 206 | 300 | 0 | 95 | 17.02 | 3.01 |
| I | Conif. Plant. | 168 | 111 | 19 | 6 | 204 | 300 | 0 | 93 | 3.59 | 1.05 |
| I | Conif. Plant. | 168 | 117 | 20 | 3 | 176 | 187 | 1 | 59 | 1.76 | 4.71 |
| I | Conif. Plant. | 154 | 165 | 21 | 3 | 220 | 56 | 1 | 55 | NA | NA |
| I | Conif. Plant. | 154 | 133 | 22 | 4 | 193 | 300 | 0 | 60 | 2.54 | 2.28 |
| I | Conif. Plant. | 168 | 124 | 23 | 4 | 209 | 146 | 1 | 85 | 1.41 | 4.64 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| J | Conif. Plant. | 163 | 174 | 24 | 5 | 237 | 300 | 0 | 63 | 2.52 | 1.07 |
| J | Conif. Plant. | 149 | 124 | 25 | 3 | 216 | 140 | 1 | 92 | 1.64 | 5.64 |
| J | Conif. Plant. | 149 | 115 | 26 | 4 | 220 | 109 | 1 | 105 | 1.11 | 5.37 |
| J | Conif. Plant. | 172 | 92 | 27 | 3 | 142 | 75 | 1 | 50 | 2.17 | 14.82 |
| J | Conif. Plant. | 163 | 119 | 28 | 6 | 193 | 162 | 1 | 74 | 1.22 | 3.78 |
| J | Conif. Plant. | 172 | 108 | 29 | 4 | 190 | 100 | 1 | 82 | 1.49 | 4.96 |
| J | Conif. Plant. | 163 | 89 | 30 | 3 | 156 | 153 | 1 | 67 | 1.70 | 5.30 |
| K | Conif. Plant. | 159 | 110 | 31 | 3 | 201 | 72 | 1 | 91 | 1.29 | 7.84 |
| K | Conif. Plant. | 159 | 263 | 32 | 4 | 339 | 119 | 1 | 76 | 2.03 | 5.76 |
| K | Conif. Plant. | 171 | 99 | 33 | 4 | 193 | 300 | 0 | 94 | 3.28 | 1.96 |
| K | Conif. Plant. | 171 | 249 | 34 | 5 | 340 | 300 | 0 | 91 | 1.25 | 1.52 |
| K | Conif. Plant. | 171 | 210 | 35 | 6 | 300 | 300 | 0 | 90 | 1.14 | 0.42 |
| K | Conif. Plant. | 145 | 95 | 36 | 6 | 195 | 300 | 0 | 100 | 1.04 | 1.39 |
| L | Partial Harvest | 147 | 127 | 37 | 3 | 236 | 300 | 0 | 109 | 1.70 | 2.25 |
| L | Partial Harvest | 160 | 142 | 38 | 3 | 208 | 300 | 0 | 66 | 2.42 | 1.22 |
| L | Partial Harvest | 160 | 119 | 39 | 4 | 165 | 300 | 0 | 46 | 5.37 | 0.88 |
| L | Partial Harvest | 147 | 137 | 40 | 5 | 247 | 300 | 0 | 110 | 1.43 | 0.57 |
| L | Partial Harvest | 147 | 109 | 41 | 4 | 232 | 300 | 0 | 123 | 7.77 | 2.51 |
| L | Partial Harvest | 160 | 167 | 42 | 6 | 281 | 300 | 0 | 114 | 2.5 | 0.37 |
| M | Partial Harvest | 152 | 103 | 43 | 5 | 197 | 175 | 1 | 94 | 2.44 | 6.77 |
| M | Partial Harvest | 152 | 325 | 44 | 3 | 384 | 255 | 0 | 59 | 2.17 | 1.78 |
| M | Partial Harvest | 152 | 105 | 45 | 6 | 185 | 107 | 1 | 80 | 1.35 | 6.26 |
| M | Partial Harvest | 166 | 224 | 46 | 4 | 297 | 106 | 1 | 73 | 1.19 | 5.05 |
| M | Partial Harvest | 166 | 137 | 47 | 5 | 234 | 300 | 0 | 97 | 2.49 | 0.89 |
| M | Partial Harvest | 152 | 122 | 48 | 3 | 197 | 74 | 1 | 75 | 1.00 | 6.78 |
| N | Partial Harvest | 170 | 92 | 49 | 6 | 170 | 127 | 1 | 78 | 1.29 | 4.85 |
| N | Partial Harvest | 170 | 173 | 50 | 3 | 271 | 300 | 0 | 98 | 2.00 | 0.79 |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| N | Partial Harvest | 170 | 224 | 51 | 5 | 309 | 300 | 0 | 85 | 2.25 | 1.02 |
| N | Partial Harvest | 156 | 176 | 52 | 5 | 275 | 300 | 0 | 99 | 1.82 | 0.89 |
| N | Partial Harvest | 156 | 137 | 53 | 3 | 213 | 300 | 0 | 76 | 1.48 | 1.02 |
| N | Partial Harvest | 170 | 178 | 54 | 4 | 273 | 300 | 0 | 95 | 11.76 | 2.47 |
| I | Conif. Plant. | 157 | 164 | 55 | 1 | 241 | 300 | 0 | 77 | NA | NA |
| I | Conif. Plant. | 152 | 130 | 56 | 1 | 190 | 198 | 1 | 60 | NA | NA |
| F | Untreated | 156 | 330 | 57 | 3 | 373 | 300 | 0 | 43 | NA | NA |
| F | Untreated | 155 | 127 | 58 | 1 | 187 | 101 | 1 | 60 | NA | NA |
| I | Conif. Plant. | 154 | 144 | 59 | 2 | 223 | 300 | 0 | 79 | NA | NA |
| F | Untreated | 156 | 107 | 60 | 2 | 175 | 80 | 1 | 68 | NA | NA |