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Conservation biology

# Narrow anthropogenic corridors direct the movement of a generalist boreal butterfly

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Ecological and anthropogenic corridors are becoming more common worldwide, but little is known about how corridor size (width) affects species' movements, and thus their effects. Here we investigated whether 4- and 8-m wide anthropogenic corridors (seismic lines) cleared for petroleum (oil sands) exploration in boreal forests in Alberta, Canada, act on altering the behaviour of a habitat generalist butterfly, the Arctic fritillary (*Boloria chariclea*). Specifically, we captured 539 Arctic fritillaries and released them in seismic line corridor or control sites with no structural directionality (i.e. forests and clearings), and recorded both their initial direction (along the seismic line or not) and persistence in directional movements. Arctic fritillaries moved inside these lines twice as often as they left them, and maintained their initial direction more often, regardless of line size and independently of forest structure or sex of individuals. Thus, anthropogenic corridors as narrow as 4 m can affect insect movements. Given the vast area of boreal forests disturbed from seismic assessments, investigating if the effects of these dense, localized lines affect population dynamics and species interactions would provide important insights to managing this ecosystem and identifying restoration actions.

## 1. Background

Anthropogenic loss of habitat has resulted in worldwide declines in biodiversity [1]. Increases in isolation of remnant patches of habitat is one mechanism contributing to biodiversity loss by negatively affecting local population sizes and species persistence [1,2]. Designing ecological corridors that link habitat remnants has, therefore, become a common mitigative tool. Previous research has shown that, by increasing suitable habitat and facilitating movement, corridors can increase landscape connectivity and sustain species richness [1,3,4]. Nevertheless, ecologists have struggled to identify generalizable responses to corridors, because corridor effects depend on the traits of species, the characteristics of the corridor and its surrounding environment, and interactive effects among species [5–7].

Anthropogenic features, such as powerlines and roads, can act as corridors directing movements of species in both positive and negative ways [4,7–9]. In the boreal forests of Alberta, Canada, narrow anthropogenic corridors referred to as 'seismic lines' (hereafter lines) are cleared of trees and shrubs across thousands of $km^2$ of forests (figure 1) to locate and map underground oil sands reserves. These lines vary in width and density, but generally occur at two different sizes: (i) 3–5 m wide lines, with local densities reaching up to 40 km $km^{-2}$, and (ii) 6–10 m wide, with densities between 1 and 5 km $km^{-2}$. Previous studies have shown that only the larger lines affect the behaviour of vertebrates, either facilitating or obstructing movements [10,11]. However, little has been done to assess behavioural responses in invertebrates, despite their sensitivity to localized changes in habitat. For butterflies, the two line

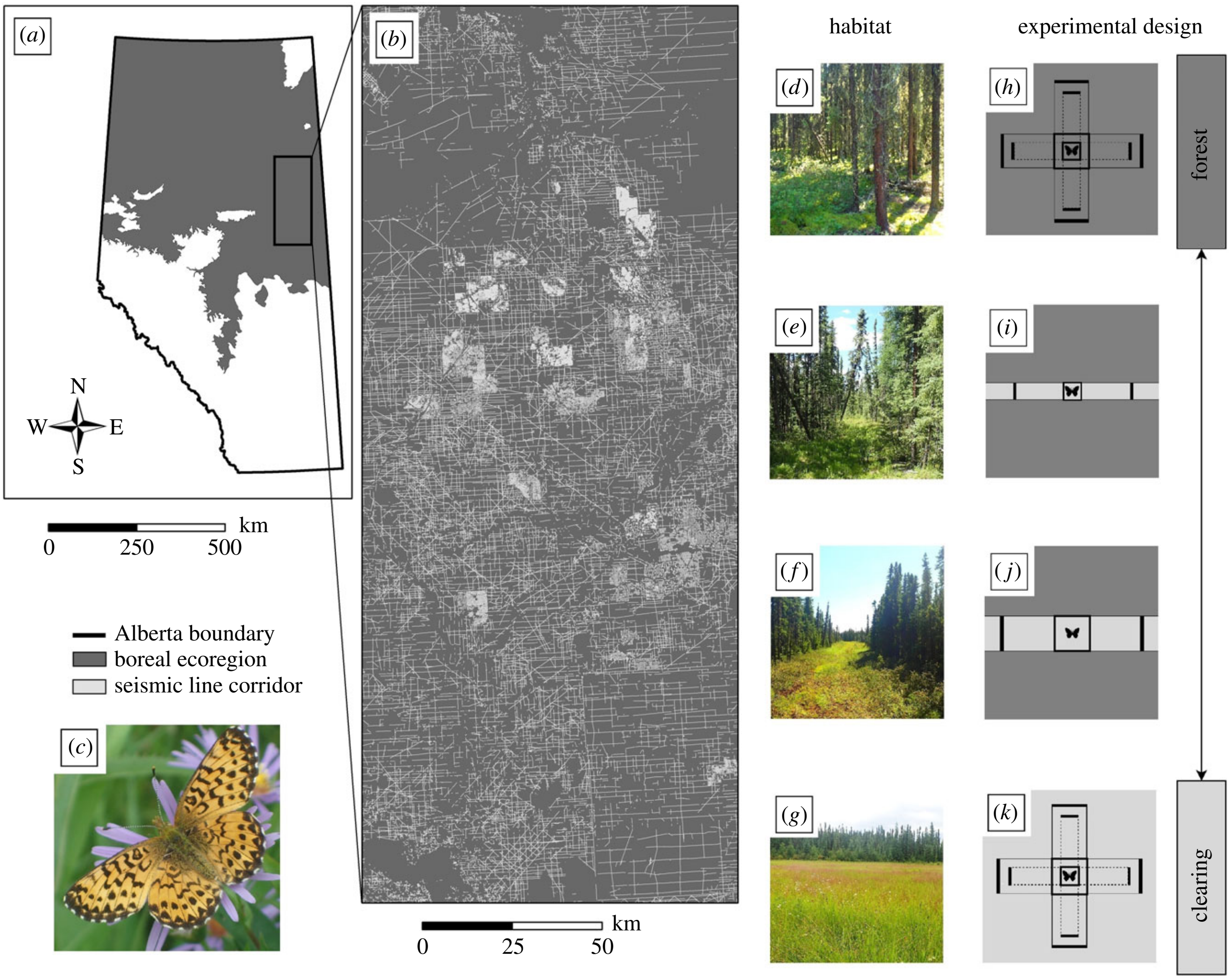


**Figure 1.** (*a*,*b*) Alberta's boreal ecoregion with the inset map illustrating the density of lines associated with oil sands assessments; (*c*) Arctic fritillary butterfly (*Boloria chariclea*); (*d*–*g*) representative images of control forest, 4- and 8-m wide lines, and control clearing, respectively; (*h*–*k*) experimental design of release arenas for four strata: control forests, 4- and 8-m wide corridors and control clearings. Lines (*i*–*j*) were assessed in both east–west and north–south directions. (Online version in colour.)

sizes differ in their effects on species composition with narrower corridors being no different from adjacent forests, while wider lines increase overall diversity and specifically the abundance of species adapted to open and early seral habitats [9]. This supports a change in perception and habitat quality for butterflies depending on line size. Nevertheless, corridors—including these anthropogenic corridors—can promote butterfly movements independent of habitat quality [12] by directing movements through changes in forest structure.

Here, we performed experimental releases of the Arctic fritillary (*Boloria chariclea*; Lepidoptera: Nymphalidae) to assess the effects of 4- and 8-m wide seismic line corridors cleared in boreal forests on the behaviour of a habitat generalist insect. Butterflies have been widely used as a model taxon for the study of landscape connectivity and corridor effects [2,8] with most finding that wider corridors enhance inter-patch movement [13], even when corridors do not provide suitable habitat [12]. Using experimental releases, we tested whether narrow (4- and 8-m wide) cleared lines in boreal forests were effective in directing the movements of Arctic fritillaries by assessing initial propensity and persistence in their directional movements. We hypothesized that Arctic fritillaries released in control sites with no structural directionality (forests and clearings) would lack directional movements due to an absence of structural cues. Conversely, butterflies released in lines were expected to follow the line direction more often due to the change in forest structure associated with these disturbances.

## 2. Material and methods

### (a) Study area and species

The study was conducted in boreal forests of the Wood Buffalo region of northeast Alberta, Canada, in coniferous treed peatlands dominated by black spruce (*Picea mariana*) and eastern larch (*Larix laricina*). Here, corridors approximately 4- or 8-m wide were cleared by industry for seismic assessments of the underground bitumen reserve, resulting in linear open (early seral forest) clearings surrounded by a matrix of mature boreal forests. See Riva *et al*. [14] for more details on the study area. Haddad [13] demonstrated that similar, but wider (32 m), corridors cleared in coniferous forests favour movements of open-habitat specialists between patches. We chose the Arctic fritillary (figure 1) because it is a generalist species in these forests (larvae feed on plants common in both corridor and forest environments, such as willows), and was the most common species in the area, being abundant in both the forest matrix and lines [14].

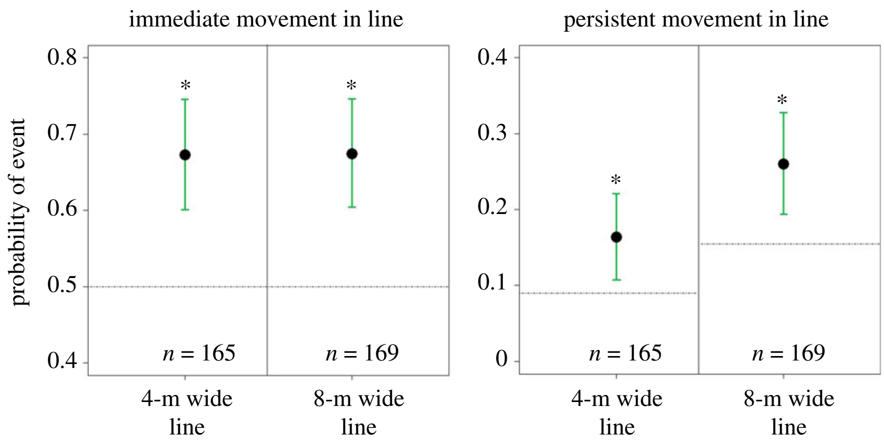


**Figure 2.** Probability of selecting the line direction when released, and persisting in the line direction after a 12-m distance, as a function of two line widths. Bars represent 95% confidence intervals. Horizontal dotted lines illustrate the expected probabilities under the null hypothesis of no preferred directionality (50% for the immediate movement; 9% or 15.5% in 4- and 8-m wide lines, respectively, for persistent flights). Asterisks represent significant differences in $\chi^2$ tests between the observed and expected probabilities of events assuming no preferred directional movement (*$p < 0.01$). (Online version in colour.)

**Table 1.** Hypothesized effect of line characteristics (width and direction), forest height, and the sex of Arctic fritillary (*Boloria chariclea*) butterflies.

| variable | hypothesized effect | rationale |
|---|---|---|
| line width | stronger effect of 8-m wide lines | narrow linear disturbances more closely resemble natural forest gaps in this system, and thus should have weaker effects than larger lines |
| line direction | stronger effect of east–west lines | tropotaxis to the sun may increase east–west line use |
| forest height | stronger effect of lines cleared in taller forests | taller forests create more distinct structural differences with that of the linear disturbance |
| forest height × line width | stronger effect of wider lines cleared in taller forests | effects of linear disturbances may be more prevalent when surrounding forests are taller creating more distinct structural differences |
| sex of individual butterflies | unknown | butterfly behaviour may vary between the sexes and this may condition responses to linear disturbances |

## (b) Experimental design

We tested the effect of 4- and 8-m wide lines on Arctic fritillary movement through experimental releases. In the summer of 2016 and 2017 we collected Arctic fritillaries, marked them to avoid re-captures, identified their sex, and released them quickly ($t < 5$ min; we assume that butterflies responded to releases with an escape flight behaviour). We controlled for temperature (greater than 17°C), hour of the day (10.00–16.00), and position of the operator releasing the butterfly (the operator laid on the ground on one of the diagonals of the release square while releasing butterflies from its waist, in the centre of the square). No significant effects of these covariates and date of release were found (electronic supplementary material).

Releases were conducted in the centre of 18 release arenas stratified in 4- and 8-m wide corridors, in both north–south and east–west directions, and in control forests and clearings without a distinct linear structure (figure 1). In each arena we set a 'release square' with two sides overlapping the corridor edges, and a 'mark' (flags) located 12 m from the release square (figure 1). Control arenas were set in analogous directions in forests and in approximately 60 × 60 m clearings that were associated with exploratory well pad openings. Upon release, butterflies were observed until they left the release arena. For each trial, we first recorded which side of the release square (box) the butterfly crossed, and then whether it persisted in its direction by crossing an additional mark set at 12 m after the release box. Because the release point is equidistant from the square sides, the probability of crossing each side is equal in the absence of directionality of movement. We assumed that after 12 m butterflies had made the choice to follow the corridor. In control arenas we emulated lines of the two sizes and directions by placing flags along the edges of the corresponding imaginary corridors (figure 1). For each butterfly released in controls, we recorded their responses for both line width scales simultaneously. Thus, when assessing controls, data were analysed as two separate subsets (4- versus 8-m scales) to ensure independence of observations.

## (c) Data analysis

Generalized linear mixed models with binomial distributions were fit in R [15]. The response variables were the binary outcomes of a butterfly leaving the release box in the corridor direction (initial direction of movement), and crossing the 12-m distance mark (persistence in directional movement). We fitted a random effect to account for dependency in releases within the same arena, and tested for the effects of treatment, corridor characteristics (width and direction), sex of butterfly, forest height (used as a proxy of forest density) and the interaction of forest height and corridor width. See table 1 for the hypothesized effect of each covariate. We then calculated the expected probabilities under the null hypothesis of no preferred directionality (electronic supplementary material), and compared these to model estimates using confidence intervals and $\chi^2$-tests.

## 3. Results

We released 539 Arctic fritillaries (29.9 ± 3.7 per arena), of which 334 were in line treatments. Model coefficients and $\chi^2$-tests are presented in the electronic supplementary material. The variance associated with the random term for arena site was less than 0.01 in all models. Control forests and clearings did not differ from the probabilities expected under a null hypothesis of no flight directionality ($\chi^2 < 1.4$, d.f. = 1, $p > 0.23$). Conversely, both line sizes demonstrated analogous, positive effects in directing butterfly movements ($\chi^2 > 6.5$, d.f. = 1, $p \leq 0.01$; figure 2), regardless of line width, forest height, and sex. Arctic fritillaries selected for line movements in 67% of the releases in both line sizes (95% CI: 60–75% for 4-m wide, and 60–74% for 8-m wide), versus the approximately 50% expected condition under the null hypothesis (figure 2). Both line types increased the probability of persistence in directional movements in comparison to controls. When released in 4-m wide lines, 16% (95% CI: 11–22%) of the Arctic fritillaries maintained the initial direction versus approximately 9% expected under the null hypothesis (figure 2). In 8-m wide lines, 26% (95% CI: 19–33%) of the butterflies maintained the initial direction versus the approximately 15.5% expected under the null hypothesis (figure 2).

## 4. Discussion

We show that both 4- and 8-m wide open (early seral) lines cleared in boreal forests for oil sands exploration conditioned the movements of Arctic fritillaries. Corridor effects were surprisingly consistent (approximately 1.5 times the expected probabilities under the null hypothesis) and independent of line width, orientation, forest structure, release arena, or sex of the butterfly, with no significant interactive effects supported (electronic supplementary material). Since butterfly assemblages in 4-m wide lines did not differ from reference control forests [14], we infer that these two environments provide similar resources for butterflies, yet respond differently in their movements. Hence, these corridor effects depended more on structural changes in habitat (i.e. forest edges) than differences in composition of vegetation (habitat), confirming that edge responses can predict movement in butterflies [16].

As for mammals [10] and birds [11], insect behaviour changes in response to these line disturbances, but here we provide the first evidence of behavioural responses to even the narrowest (less than 5-m wide) open forest disturbances. Although using narrower lines mitigates the effects of seismic exploration on boreal forest habitat and species composition (e.g. [11,14]), it still affects movements of butterflies. Since we used a generalist species that does not avoid the forest matrix, we suggest that many other insects, particularly early seral specialists (e.g. most boreal butterflies [14] and pollinators) are likely responding to these lines. Given the sheer scale of these disturbances (thousands of km$^2$ of forests disturbed, with local corridor densities of up to 40 km km$^{-2}$), and the documented, multiple effects of corridors on species abundance, persistence, and species interactions [4,5,7–9], we recommend further study into whether the observed behavioural responses affect population dynamics, species persistence, or trophic interactions (e.g. pollination network). Increases in movements would potentially increase habitat connectivity, and thus population viability through changes in gene flow and re-colonization of unoccupied patches (rescue effects). It may, however, also entail greater risks to populations by increasing the spread of antagonistic or invasive species, edge effects, or synchronization of populations. This is true not only for butterflies and other invertebrates, but also more broadly for vertebrates and plants [2,3,7].

Linear infrastructures, such as power lines and roads, are a primary source of habitat fragmentation worldwide [9]. Our study demonstrates that even very narrow linear disturbances, such as seismic lines used to explore oil, can trigger behavioural responses in butterflies, and presumably other insects. Given the current rate of habitat loss and degradation associated with linear features, understanding when and how corridors work is a conservation priority—both for designing ecological corridors, and in understanding the effects of anthropogenic linear disturbances on populations and biodiversity. Fragmentation effects may be strong despite limited amounts of habitat disturbed (in Alberta, generally less than 15% of boreal forests [14]).

Data accessibility. Data and R script are available as electronic supplementary material.

Authors' contributions. All authors designed the experiment. F.R. performed the experiment and analyses. F.R. wrote the manuscript with S.E.N. and J.H.A. assistance. All authors approve the final version of the manuscript and agree to be accountable for all aspects of this work.

Competing interests. We declare that we have no competing interests.

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