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Perceptual Range, Targeting Ability, and Visual Habitat Detection by Greater Fritillary Butterflies *Speyeria cybele* (Lepidoptera: Nymphalidae) and *Speyeria atlantis*

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Abstract

Butterflies are widely invoked as model organisms in studies of metapopulation and dispersal processes. Integral to such investigations are understandings of perceptual range; the maximum distance at which organisms are able to detect patches of suitable habitat. To infer perceptual range, researchers have released butterflies at varying distances from habitat patches and observed their subsequent flight behaviors. It is often assumed that butterflies rely on visual senses for habitat detection; however, this assumption has not been explicitly investigated. Here, we assess the extent and sensory determinants of perceptual range for the great spangled fritillary (*Speyeria cybele* (Fabricius, 1775)) and Atlantis fritillary (*Speyeria atlantis* (W.H. Edwards, 1862)). This was achieved by experimentally releasing butterflies over open water at various distances from a lake island, representing an isolated habitat patch in a dichotomous habitat-matrix landscape. To infer whether butterflies rely on vision for habitat detection, we exposed a subset of butterflies to a series of intense light flashes before release to induce flash blindness (bleaching of photoreceptive rhodopsins) without affecting olfaction. Flashed individuals were 30.1 times less likely to successfully navigate to the target island after release, suggesting butterflies rely primarily on visual senses to navigate fragmented landscapes. For unflashed butterflies, the likelihood of successful navigation decreased by a factor of 2.1 for every 10 m increase in release distance. However, no specific distance threshold for perceptual range was observed. We therefore suggest that perceptual range is best viewed as a continuum of probabilities (targeting ability), reflecting the likelihood of habitat detection across a range of distances.

Key words: perceptual range, perceptual grain, habitat fragmentation, dispersal, flight behavior

The movement of organisms between patches of suitable habitat is a principal ecological process contributing to both metapopulation persistence and diversity patterns on fragmented landscapes (Hanski 1998, Wiens 2001, Stevens et al. 2012). Butterflies (Lepidoptera: Papilionoidea), in particular, have proven to be important model organisms in related studies, as their adult movements are easily observable (e.g., Haddad 1999, Dover and Fry 2001, Riva et al. 2018), individuals may be marked for recapture (e.g., Ehrlich and Davidson 1960, Baguette 2003, Nowicki et al. 2014), and patch occupancy may be inferred due to their high detectability and well-documented host plant relationships (e.g., Hanski et al. 1996; Tiple et al. 2011; MacDonald et al. 2017, 2018a; Grant et al. 2018). However, despite a considerable history of study, information is generally lacking on how butterflies actually detect and navigate to patches of suitable habitat while moving through matrices of unsuitable habitat (Baguette and Van Dyck 2007, Schtickzelle et al. 2007). Related

investigations are often predicated on estimating butterfly perceptual range; the maximum distance at which individuals are able to detect patches of suitable habitat using their sensory organs (Wiens 1989).

To estimate perceptual range, butterflies may be released at varying distances from habitat edges, and their flight behaviors subsequently observed. Employing these or related methods, the perceptual ranges of multiple butterfly species have been estimated: the bay checkerspot (*Euphydryas editha bayensis* Sternitzky, 1937) at 50 m (Harrison 1989); the sleepy orange (*Eurema nicippe* (Cramer, 1779) (Lepidoptera: Pieridae)) and cloudless sulphur (*Phoebis sennae* (Linnaeus, 1758) (Lepidoptera: Pieridae)), both at 8 m (Haddad 1999); the Fender's blue (*Icaricia icarioides fenderi* (Macy, 1931) (Lepidoptera: Lycaenidae)), between 10 and 22 m (Schultz et al. 2001); the bog fritillary (*Boloria* [*Proclossiana*] *eunomia* (Esper, 1800) (Lepidoptera: Nymphalidae)), between 15 and 30 m (Schtickzelle et al. 2007); and the speckled wood (*Pararge aegeria*

(Linnaeus, 1758) (Lepidoptera: Nymphalidae)), at either 50 or 100 m, depending on whether individuals originated from fragmented or contiguous landscapes, respectively (Merckx and Van Dyck 2007). Contrasting with these studies, Fahrig and Paloheimo (1987) observed that female cabbage white butterflies (*Pieris rapae* (Linnaeus, 1758) (Lepidoptera: Pieridae)) did not orient towards patches of their host plants from distances greater than 1 m. While this was interpreted as evidence that visual senses of *P. rapae* are quite limited (Fahrig and Paloheimo 1987), it is unclear whether patches of host plants contrasted visually with the matrix in which butterflies were released, and whether the experiment facilitated use of olfactory senses.

Taken together, results of these studies demonstrate that perceptual ranges of butterflies are both variable and considerable, despite limitations of the compound eye (Rutowski 2003). Indeed, structural properties of butterfly ommatidia suggest that even large objects, several meters high, may not be resolvable at distances greater than 20–30 m (Rutowski 2003). Other senses, namely olfaction, may account for detection of suitable habitat and nectar resources beyond these distances (Cardé and Willis 2008). At finer spatial scales, visual and olfactory senses may work synergistically in larval host plant detection. For example, studies addressing the pipevine swallowtail (*Battus philenor* (Linnaeus, 1771) (Lepidoptera: Papilionidae)) in southeast Texas suggest that, while females identify suitable larval host plants by visual recognition of leaf shapes (Rausher 1978), individuals develop relevant search images by building associations between leaf shapes and appropriate chemical compositions (Papaj 1986). Other investigations of butterflies' senses and their relationships to habitat or resource detection have been largely limited to comparisons of genetic and morphological traits among species, populations, sexes, or individuals that differ in movement, dispersal, or migratory behaviors (e.g., Hill et al. 1999, Berwaerts et al. 2006, Niitepõld et al. 2009, Altizer et al. 2010, Turlure et al. 2016; reviews in Silberglied 1984, Weiss 2001).

Despite this considerable body of literature, little has been done to experimentally decouple contributions of butterflies' multiple senses to detecting patches of suitable habitat while moving through matrices of unsuitable habitat. Offering some insight, Dover and Fry (2001) simulated suitable habitat corridors (hedgerows) in an agricultural landscape using windbreak materials, and passively observed flight behaviors of passing butterflies, including the scarce copper (*Heodes virgaureae* (Linnaeus, 1758) (Lepidoptera: Lycaenidae)), heath fritillary (*Mellicta athalia* (Rottemburg, 1775) (Lepidoptera: Nymphalidae)), high brown fritillary (*Argynnis* [Fabriciana] *adippe* (Dennis & Schiffermüller, 1775) (Lepidoptera: Nymphalidae)), and niobe fritillary (*Argynnis* [Fabriciana] *niobe* (Linnaeus, 1758) (Lepidoptera: Nymphalidae)). Their erected structures resembled habitat visually, but not chemically, and were still observed to influence flight patterns. This suggests that butterflies rely at least partially on visual senses to detect suitable habitat. However, individuals were only observed to fly along simulated hedgerows when they were encountered, and specific distances at which butterflies responded to or oriented towards hedgerows were not reported.

In this study, we investigated the extent and sensory determinants of perceptual range for two species of greater fritillary butterflies, the great spangled fritillary (Speyeria cybele (Fabricius, 1775) (Lepidoptera: Nymphalidae)) and Atlantis fritillary (*Speyeria atlantis* (W.H. Edwards, 1862) (Lepidoptera: Nymphalidae)), occurring in the Lake of the Woods region, Ontario, Canada. On islands of Lake of the Woods, *S. cybele* and *S. atlantis* have been observed to consistently avoid open water during flight movements, indicating that they perceive islands as discrete patches of suitable habitat situated in a matrix of unsuitable habitat (Z. G. MacDonald, unpublished data, and see MacDonald et al. 2018a). Preferred larval host plants of *S. cybele* and *S. atlantis* are *Viola* species. While *Viola* commonly occur on these islands (MacDonald et al. 2018b), we cannot be sure whether host plants exist in sufficient quantities within single islands to sustain isolated populations. Notwithstanding, we define islands as suitable habitat under the functional resource-based concept (sensu Dennis et al. 2003), as each contains resources sufficient for mate location, resting, roosting, feeding, and predator escape. Under this habitat concept, the open-water matrix is entirely unsuitable. The high-contrast nature of this relatively dichotomous habitat-matrix system thereby serves as a suitable natural arena for inferring perceptual range via experimental releases. Furthermore, the open-water matrix controls for unwanted matrix heterogeneity that might affect butterfly flight behavior (e.g., Nowicki et al. 2014).

To estimate perceptual range of both *S. cybele* and *S. atlantis*, we released individuals over open water at varying distances from a single island and observed their flight behaviors. To investigate the extent to which butterflies rely on visual senses to detect and navigate to patches of suitable habitat during dispersal movements, we developed a novel method of exposing individuals' photoreceptors to a series of intense light flashes before release. We hypothesized that this method would induce flash blindness through bleaching of photoreceptive pigments (rhodopsins; e.g., Bernard 1983a,b, Briscoe et al. 2003), reducing butterflies' ability to detect and navigate to the target island. Such a result would suggest visual senses are a primary means by which *S. cybele* and *S. atlantis* detect and navigate to patches of suitable habitat while moving through matrices of unsuitable habitat.

Methods

Study Area and Experimental Design

Our study area was located at the southeast corner of Lake of the Woods, Ontario, Canada. We collected a total of 41 *S. cybele* and 54 *S. atlantis* at three mainland sites within 20 km of Morson, Ontario, between 1 July and 30 July 2016. All collected specimens were judged to be in good condition with minimal wear to wing margins. Collection of specimens was completed between 10:00 and 14:00 on days with ambient temperatures above 20°C, cloud cover less than 75%, and wind speeds below 25 km h⁻¹. Collection sites were located at least 10 km from the lake shore, and were equivalent in habitat composition and structure, comprised of meadows situated within mixed stands of boreal and laurentian tree species (e.g., *Pinus strobus*, *P. banksiana*, *Betula papyrifera*, *Acer spicatum*, *Picea glauca*, and *Tilia americana*). After collection, butterflies were temporarily housed in small, polypropylene containers, kept within a cooler maintained between 20 and 25°C. Collected butterflies were then immediately transported via motorboat to a single island, located at 49.1139° N, –94.2071° E, for experimental release on the same day as collection. This 'target' island is approximately 1.0 ha in area, and was specifically selected for experimental releases because of its approximately circular shape, uniform habitat composition (mixed woodland and shoreline meadow), uniform habitat height (~25 m), and considerable isolation from other landmasses (>300 m). We secured the boat's position at varying distances from the target island's shore (30, 40, 50, or 60 m), using a laser range finder (RX-1200i TBR DNA; Leupold & Stevens, Inc., Beaverton) and a combination of anchors and a stern tie. For all releases, the boat was positioned relative to the target island such that the bearing to the island's center was 90° to the wind direction (Fig. 1). This
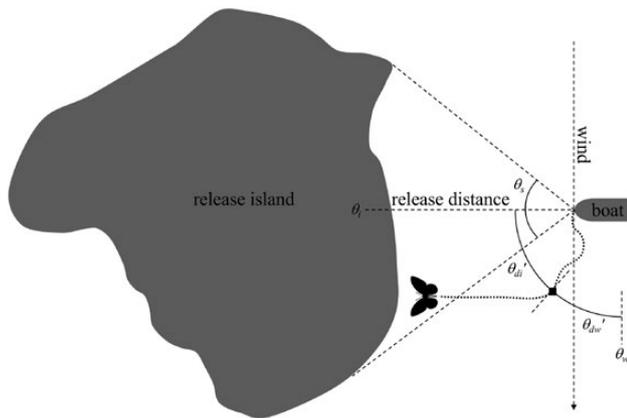
Fig. 1. Visual representation of experimental releases. The boat was secured at varying distances from the target island's shore (30, 40, 50, or 60 m), such that the bearing to the island's center was 90° to the wind direction. Butterflies were sexed, marked, and released one at a time. For each released individual, flight time and flight orientation at 2.5, 5, and 10 m of travel were recorded. Angular subtense of the target island, θ_s, was estimated as the angular difference between the left and right shore bearings. Deviations in flight orientations from wind direction (θ_w) and island direction (θ_i), given by θ_{dw}' and θ_{di}', respectively, were estimated at 2.5, 5, and 10 m of travel using eq. 2 (see Methods).

effectively controlled for biases that may arise from butterflies being blown towards or away from the island after their release, changing the effective release distance.

Once the boat was secured at specific distances from the target island, butterflies were sexed, marked, and released one at a time. All releases were completed between 14:00 and 18:00 on days with ambient temperatures above 20°C, cloud cover less than 75%, and wind speeds below 25 km h⁻¹. Each butterfly was released from a 1.5-m aerial net, held away from the edge of the boat towards the target island's center. Keeping as still as possible, the extended net was left open for butterflies to leave at their own will. A second observer recorded the emerging orientation of butterflies, as well as their total flight time and flight orientation after 2.5, 5, and 10 m of travel. Each butterfly was then visually tracked, using a binocular, until it successfully navigated to the target island or flew out of sight (at distances greater than 100 m).

To investigate the role of vision in habitat detection, we sought to devise a method to inhibit butterflies' visual senses without affecting their other senses or flying ability. Painting over, or otherwise covering, butterflies' compound eyes would not achieve this, as this would introduce chemical compounds to sensory areas and add mass to the butterfly itself. To avoid these confounds, we attempted to induce flash blindness by exposing butterflies' photoreceptors to a series of intense light flashes before release. A powerful external photographic flash was used as a flash source (EM-140 DG Macro Flash, guide number = 14 at ISO 100, Sigma Corporation, Kawasaki, Japan). Triggering the flash for 1/6,000 s at a distance of 10 cm produced an estimated 100,352,000 lux (lumens m⁻²); approximately 1,024 times the intensity of ambient sunlight. Flashing butterflies at 10 cm from the left, right, dorsal, ventral, posterior, and anterior surfaces of their compound eyes, such that the majority of ommatidia were directly exposed to the flash. Butterflies were kept in their polypropylene containers within a dark cooler before flashing to maximize deleterious effects of flashing on rhodopsins (Bernard 1983a,b, Briscoe et al. 2003). Approximately half of *S. cybele* and *S. atlantis* released at each distance were flashed immediately before release.

Flash blindness is caused by bleaching of rhodopsins involved in visual phototransduction within rhabdomeres (Przewłocki et al. 1983). Past work has shown that exposing butterflies' compound eyes to repeated flashes may bleach rhodopsins either temporarily or permanently, depending on the number and intensity of flashes (Bernard 1983a,b, Briscoe et al. 2003). It is also reported that butterfly rhodopsins involved in the detection of ultraviolet, blue, green, and red light are all susceptible to bleaching (Bernard 1983a,b, Briscoe et al. 2003). We did not complete work to assess whether this flash method induced temporary or permanent bleaching of rhodopsins (i.e., temporary or permanent flash blindness). However, if flashed butterflies consistently failed to detect and navigate to the target island from distances at which unflashed butterflies were generally successful, it would be reasonable to conclude that: 1) the flash method effectively inhibited butterfly photoreceptor function through bleaching of rhodopsins, resulting in flash blindness and 2) *Speyeria* spp. rely primarily on visual senses to detect and navigate to patches of suitable habitat while moving through matrices of unsuitable habitat.

Data Analyses

A series of generalized linear models (GLMs) were used to assess what environmental and organism-specific variables affected butterflies' probability of successful navigation, flight speed and tortuosity, and flight orientation. All statistical analyses were performed using the statistical software R version 3.4.3 (R Core Team, 2017).

Probability of Successful Navigation

Model 1: Binomial GLMs (logit link) were used to measure the effects of release distance, wind speed, species identity, sex, and visual impairment (flashing) on the probability of successfully navigating to the target island (success/failure). Interactions between relevant experimental variables were assessed using first-degree interaction terms. Sunlight (direct vs diffuse), percentage cloud cover (estimated as 1—proportion of blue sky visible to observers), ambient temperature, butterfly collection location, day of release, and time in captivity were included as noise variables. All experimental variables were fitted regardless of their significance, with relevant interaction terms and noise variables included in the final model only if significant. Standardized coefficients were estimated for all continuous variables. To interpret the effects of experimental variables on the likelihood of navigation success, odds ratios were estimated using original units of experimental variables to permit straight-forward interpretation.

Model 2: Perceptual ranges of butterflies are most often reported as a single distance measures, irrespective of patch size or habitat characteristics (e.g., Harrison 1989, Schultz et al. 2001, Merckx and Van Dyck 2007, Schtickzelle et al. 2007). However, analyses of butterflies' ommatidial structures suggest that the sizes of objects may determine the maximum distances at which they are detectable (i.e., single object thresholds; Rutowski 2003). Therefore, the ability to detect habitat patches may decrease with increasing distance simply because of decreasing angular subtense, rather than increasing distance per se. To decouple these variables, we estimated the angular subtense of the target island for each experimental release as the angular difference between the left and right shore bearing (Fig. 1). Although the target island was approximately circular in shape, angular subtense still varied independent of release distance, depending on the location of the release boat (i.e., the direction from which the island was viewed). As would be expected, angular subtense and release distance were negatively correlated ($r = -0.775$). This strong correlation limited our

ability to partition variance in the probability of successful navigation between angular subtense and release distance using residual or multiple regression techniques (Freckleton 2002). However, if sizes of habitat patches or islands determine the maximum distances at which they are detectable, a competing model accounting for angular subtense should explain more variation in navigation successes than a model accounting for release distance. We tested this hypothesis by substituting the target island's angular subtense into the previous binomial GLM built using release distance. The significance of the two variables, as well as McFadden's pseudo R^2, was compared between the two competing models.

Flight Speed and Tortuosity

Models 3 and 4: GLMs were next used to measure the effects of release distance, wind speed, species identity, sex, and flashing on: 1) flight speed, estimated as total flight time after 10 m of travel and 2) flight tortuosity, estimated as the standard deviation of turn angles between first emergence, 2.5, 5, and 10 m of travel. Calculating the standard deviation of turn angles is nontrivial, since bearings wrap from 359° around to 0° (Batschelet 1981). Therefore, to estimate turn angles ($\theta_d{'}$), we standardized flight orientations at each distance (2.5, 5, and 10 m; θ_d) relative to flight orientations at the previous distance (emergence, 2.5, and 5 m; θ_{d-1}), using the following conditional equation (eq. 1):

$$\theta'_d = \begin{cases} \theta_d - \theta_{d-1}, & |\theta_d - \theta_{d-1}| \leq 180° \\ \theta_d - \theta_{d-1} + 360°, & \theta_d - \theta_{d-1} < -180° \\ \theta_d - \theta_{d-1} - 360°, & \theta_d - \theta_{d-1} > 180° \end{cases}$$

This equation produces reliable turn angle estimates, so long as absolute differences in sequential flight orientations are less than 180°, which they were in all instances. Within flight speed and flight tortuosity GLMs, experimental variables were fit regardless of their significance, with relevant interaction terms and noise variables included only if significant. Success/failure of navigation to the target island was fit as a binary covariate in both models, to assess whether flight speed and tortuosity varied between butterflies that were successful and unsuccessful in navigating to the target island. Total flight time after 10 m of travel and standard deviations of turn angles both took on positive continuous values that were best fit using a gamma distribution (log link).

Determinants of Flight Orientation

Models 5 and 6: Perceptual range is often inferred by determining the maximum distance at which the proportion of released butterflies orienting towards habitat significantly differs from what is expected under random flight orientations (e.g., Fahrig and Paloheimo 1987, Schtickzelle et al. 2007). Specifically, this random flight null assumption assumes that the proportion of butterflies failing to detect the a nearby habitat patch, but still flying towards it, will be proportional to the angular subtense of the patch divided by 360°. However, contrasting with this null assumption, wind direction appeared to determine initial flight orientations for the majority of released butterflies in our study, independent of whether butterflies detected and navigated to the target island or not. If wind direction indeed determined the flight orientations of the majority released butterflies, the proportion of butterflies failing to detect a habitat patch, but still flying towards it, will be less than what is predicted by the random flight null assumption.

As a corollary of these relationships, we expect that, for butterflies that successfully detected and navigated to the target island (hereafter,

'successful butterflies'), deviations in flight orientations from wind direction should increase with distance flown, while deviations in flight orientations from island direction should decrease with distance flown. Such relationships correspond to reorientation away from the wind direction, towards the target island. This reorientation is not predicted for butterflies that were unsuccessful in detecting and navigating to the target island ('unsuccessful butterflies'), and deviations in flight orientations from wind direction and island direction should not vary with distance flown. To build statistical models to test these predictions, we first estimated: 1) absolute deviations in flight orientations at 2.5, 5, and 10 m (θ_d) from wind direction (θ_w), given by $\theta_{dw}{'}$ and 2) absolute deviations in flight orientations at 2.5, 5, and 10 m (θ_d) from the bearing to the center of the target island (θ_i), given by $\theta_{di}{'}$. This was achieved using the following conditional equation (eq. 2):

$$\theta'_{dx} = \begin{cases} |\theta_d - \theta_x|, & |\theta_d - \theta_x| \leq 180° \\ |\theta_d - \theta_x + 360°|, & \theta_d - \theta_x < -180° \\ |\theta_d - \theta_x - 360°|, & \theta_d - \theta_x > 180° \end{cases}$$

where θ_w or θ_i takes the place of θ_x and $\theta_{dw}{'}$ or $\theta_{di}{'}$ takes the place of $\theta_{dx}{'}$ for estimating deviations in flight orientations from wind direction or island direction, respectively. Two generalized linear mixed models (GLMMs) were used to assess whether: 1) deviations in flight orientations from wind direction increased with distance flown and 2) deviations in flight orientations from island direction decreased with distance flown. Dependent variables used in these GLMMs were: 1) absolute deviations in flight orientations from wind direction and 2) absolute deviations in flight orientations from island direction. Experimental variables in both GLMMs included distance flown (2.5, 5, and 10 m), wind speed, and success/failure of navigation to the target island. Release ID was treated as the random effect within GLMMs to control for lack of independence between successive flight orientations of individuals. An interaction term between distance flown and success/failure was used to assess whether relationships between deviations in flight orientations and distance flown differed between successful and unsuccessful butterflies. Flashed butterflies were not included within GLMMs to avoid introducing unwanted noise in flight orientations. Tweedie distributions (log link) were used to accommodate non-negative continuous response variables and right skew (Dunn and Smyth 2005).

Within the first GLMM, a significant positive interaction between distance flown and success would indicate that deviations in flight orientations from wind direction increased with distance flown for successful butterflies. Within the second GLMM, a significant negative interaction between distance flown and success would indicate deviations in flight orientations from island direction decreased with distance flown for successful butterflies. Nonsignificant main effects of flight distance in both models would suggest that these relationships were only observed for successful butterflies, that is, deviations in flight orientations from wind direction and island direction were unrelated to distance flown for unsuccessful butterflies. Together, these results would indicate that instances of successful navigation generally involved a reorientation away from wind direction and towards island direction after release, questioning the validity of the random flight null assumption.

Results

Probability of Successful Navigation

For both *S. cybele* and *S. atlantis*, the proportion of unflashed butterflies successfully navigating to the target island generally decreased
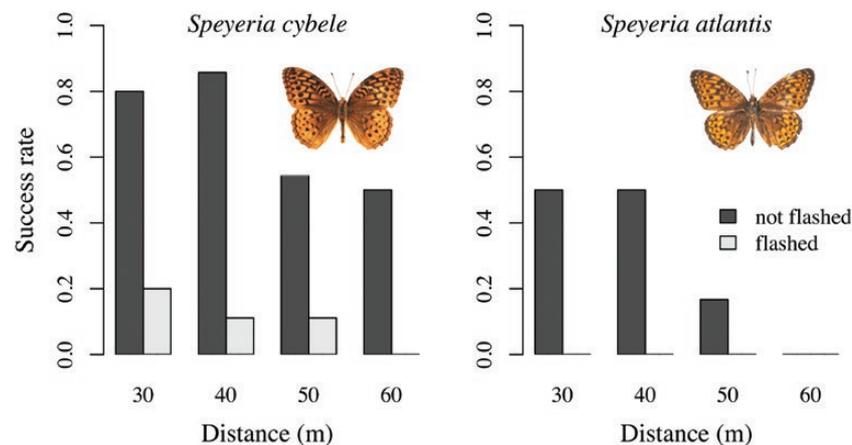
Fig. 2. The proportion (success rate) of *Speyeria cybele* and *Speyeria atlantis* that successfully navigated to the target island after experimental release at 30, 40, 50, and 60 m. Flashed butterflies were exposed to a series of intense flashes immediately before release. This method induced flash blindness through bleaching of photoreceptive rhodopsins, without affecting olfaction. Reduced success rates of flashed butterflies indicate that butterflies rely primarily on visual senses to detect and navigate to suitable habitat patches during interpatch and dispersal movements.

with increasing release distance (Fig. 2). At the maximum release distance of 60 m, 50.0% of unflashed *S. cybele* were successful (Table 1). At 50, 40, and 30 m, 54.5, 85.7, and 80.0% of unflashed *S. cybele* were successful. At 60 m, no unflashed *S. atlantis* were successful. This increased to 16.7% at 50 m, and to 50.0% at both 40 and 30 m. Flashing substantially reduced percentages of successful navigation for both species at all distances. Considering all releases at all distances, only 11.1% of flashed *S. cybele* and no flashed *S. atlantis* were successful in navigating to the target island. This contrasts with the 66.6% of unflashed *S. cybele* and 33.3% of unflashed *S. atlantis* that were successful in navigating to the target island overall.

The first binomial GLM accounting for probability of successful navigation to the target island corroborated these relationships (Model 1, Table 2). Release distance had a significant negative effect on the probability of successful navigation. An odds ratio of 0.93 (95% confidence interval [CI]: 0.87, 0.98) indicates that the likelihood of successful navigation decreased by a factor of 1.08 for every 1 m increase in release distance, or by a factor of 2.15 for every 10 m increase in release distance. The effect of an interaction between species and distance was nonsignificant, suggesting that decreases in the likelihood of successful navigation associated with increases in release distance were approximately equivalent between species. However, *S. cybele* had a significantly higher probability of successful navigation than *S. atlantis* overall. An odds ratio of 2.48 (95% CI: 0.76, 9.13) indicates that released *S. cybele* were 2.48 times more likely to successfully navigate to the target island than *S. atlantis*. No significant difference between sexes was observed. Flashing butterflies had a significant negative effect on the probability of successful navigation. An odds ratio of 0.03 (95% CI: 0.01, 0.13) indicates that flashed butterflies were 30.13 times less likely to successfully navigate to the target island than unflashed butterflies. Substituting angular subtense of the target island into the binomial GLM accounting for release distance reduced model fit (McFadden's pseudo R^2: Model 1 = 0.36; Model 2 = 0.31), and angular subtense was not significantly related to the probability of successful navigation (Model 2, Table 2).

Flight Speed and Tortuosity
Wind speed was observed to have a significant negative effect on flight time after 10 m, indicating that higher wind speeds were generally associated with faster movement (Model 3, Table 2).

Flashing butterflies had a significant positive effect on flight time to 10 m, indicating that flashed butterflies generally flew slower than unflashed butterflies. Flight time to 10 m was not observed to significantly relate to release distance, species, sex, or eventual success/failure of navigation to the target island.

Flight tortuosity, measured as the standard deviation of turn angles for each individual, significantly decreased with increasing wind speed (Model 4, Table 2). Flashing had a significant positive effect on flight tortuosity. These results, in combination with those of the flight speed model (Model 3), suggest that: 1) higher wind speeds were generally associated with faster, less tortuous flights and 2) flashed butterflies exhibited slower, more tortuous flights than unflashed butterflies. The positive relationship between success and flight tortuosity (Model 4) suggests that flight paths of successful butterflies were significantly more tortuous than those of unsuccessful butterflies. This is consistent with the hypothesis that instances of successful navigation generally involved reorientation from wind direction to island direction, increasing observed tortuosity. *S. cybele* may have exhibited more tortuous flights on average than *S. atlantis*, but this effect was only significant at $\alpha = 0.10$ ($P = 0.058$). Flight tortuosity did not significantly vary with release distance or sex. The effects of relevant interactions and noise variables in Models 3 and 4 were nonsignificant.

Determinants of Flight Orientation
GLMMs accounting for absolute deviations in flight orientations from wind direction (Model 5; Table 2) and island direction (Model 6; Table 2) each indicated that both wind speed and success were significantly related to flight orientations. Wind speed was observed to have a significant negative effect on absolute deviations in flight orientations from wind direction, and a significant positive effect on absolute deviations in flight orientations from island direction. Flight orientations of successful butterflies were significantly nearer to island direction and further from wind direction than unsuccessful butterflies.

Within the GLMM accounting for absolute deviations in flight orientations from wind direction (Model 5), the positive interaction between distance flown and success suggests that deviations in flight orientations from wind direction increased with distance flown for successful butterflies. This interaction was, however, only significant at $\alpha = 0.10$ ($P = 0.068$). Within the GLMM accounting for deviations

Table 1. The number of *Speyeria cybele* and *Speyeria atlantis* released at 30, 40, 50, and 60 m that were successful and unsuccessful in navigating to the release island

Release distance (m)	Navigation to island	*Speyeria cybele*		*Speyeria atlantis*	
		Not flashed	Flashed	Not flashed	Flashed
30	Successful:	4	1	4	0
	Unsuccessful:	1	4	4	6
40	Successful:	6	1	3	0
	Unsuccessful:	1	8	3	6
50	Successful:	6	1	1	0
	Unsuccessful:	5	8	5	3
60	Successful:	2	0	0	0
	Unsuccessful:	2	4	4	2

A subset of butterflies were exposed to a series of intense flashes immediately before release. This method induced flash blindness through bleaching of photo-receptive rhodopsins, without affecting olfaction.

Table 2. Summary of GLM and GLMM results

Dependent variable	Experimental variables					
	Release distance[1]	*Wind speed*[2]	*Species*[3]	*Sex*[4]	*Flashing*[5]	
Model 1: navigation success	−0.777*	0.024	2.117**	0.909	−3.405***	
	Angular subtense[6]	*Wind speed*	*Species*	*Sex*	*Flashing*	
Model 2: navigation success	0.378	−0.136	1.750**	0.780	−3.132***	
	Release distance	*Wind speed*	*Species*	*Sex*	*Flashing*	*Success*[7]
Model 3: flight speed	0.049′	−0.200***	−0.041	0.071	0.226***	0.111
Model 4: flight tortuosity	0.066	−0.522***	0.405′	−0.177	0.540*	0.524*
	Distance flown[8]	*Wind speed*	*Species*	*Sex*	*Success*	*Distance flown × success*
Model 5: deviation from wind direction	−0.025	−0.523***	0.155	−0.115	0.537*	0.190′
Model 6: deviation from island direction	0.017	0.158**	0.054	−0.129	−0.429***	−0.176***

Coefficient estimates and their corresponding *P*-values are given in parentheses. Coefficient estimates for continuous variables (release distance, wind speed, angular subtense, and distance flown) are standardized. Models 1 and 2 (GLMs) were fitted using a binomial distribution with a logit link function. Navigation success was measured as the success or failure of navigation to the release island. Models 3 and 4 (GLMs) were fit using a gamma distribution with a log link function. Flight speed was measured as total flight time to 10 m. Flight tortuosity was measured as the standard deviation of turn angles. Models 5 and 6 (GLMMs) were fitted using a Tweedie distribution with a log link function. Deviation from wind direction and deviation from island direction were measured as absolute deviations in flight orientations from the wind bearing and the bearing towards the release island's center, respectively, after 2.5, 5, and 10 m of flight. Individual ID was treated as a random effect to account for lack of independence between successive flight orientations of individuals.

[1]Continuous: distance at which butterflies were released from the island (m); [2]continuous: wind speed at time of release (kmph); [3]categorical: *S. cybele* or *S. atlantis*, with *S. atlantis* treated as the reference category; [4]categorical: male or female, with females treated as the reference category; [5]categorical: exposure to a series of flashes to induce flash blindness (see Methods), with flashing treated as the reference category; [6]continuous: difference between the left and right shore bearings of the release island estimated for each release; [7]categorical: eventual success/failure of navigation to the release island, with failure treated as the reference category; [8]continuous: distance travelled by butterflies from the release boat after release (2.5, 5, or 10 m). Significance is denoted by: ′$P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

in flight orientations from island direction (Model 6), the negative effect of the interaction between distance flown and success indicated that deviations in flight orientations from island direction decreased with distance flown for successful butterflies. The main effects of distance flown on absolute deviations in flight orientations from both wind direction and island direction were near zero and nonsignificant in Models 5 and 6. Collectively, these results indicate that successive flight orientations of successful butterflies, but not unsuccessful butterflies, tended away from the wind direction and towards the island direction as butterflies travelled further from the release location. Therefore, instances of successful navigation generally involved a reorientation from wind direction to island direction after release. Flight orientations of unsuccessful butterflies were almost always aligned with the wind direction until they drifted out sight.

Discussion

Quantifying Perceptual Range

As expected, the probability of *S. cybele* and *S. atlantis* successfully detecting and navigating to the target island significantly decreased with increasing release distance. The effect of release distance on probability of success was substantial, with the likelihood of butterflies successfully navigating to the target island decreasing by a factor of 2.15 for every 10 m increase in release distance. Similar observations have led many ecologists to infer the existence of maximum distance thresholds, beyond which, butterflies are unable to detect habitat patches or habitat features using their sensory organs. Based on such thresholds, Schtickzelle et al. (2007) and Dover and Settele (2009) suggest that a distinction between 'apparent fragmentation' and 'functional fragmentation' may be meaningful. While apparent fragmentation may describe any landscape with discrete habitat patches, functional fragmentation is reserved for landscapes wherein interpatch distances exceed the perceptual ranges of focal taxa (Dover and Settele 2009).

In the context of this framework, single distance measures of perceptual range are appealing due to the relative simplicity of applying specific thresholds of patch isolation to infer whether landscapes are functionally fragmented—ecologists need only estimate single distance measures of perceptual range for focal taxa. For butterflies, in particular, a straight-forward method has been to determine the

maximum distance at which the proportion of released individuals orienting towards habitat significantly differs from what is expected given random flight orientations (i.e., a random flight null assumption; e.g., Fahrig and Paloheimo 1987, Merckx and Van Dyck 2007, Schtickzelle et al. 2007). However, in this study, GLMMs (Models 5 and 6) suggested that instances of successful navigation generally involved a reorientation from wind direction (not random direction) to island direction after release. For unsuccessful butterflies, the mean of absolute deviations in flight orientations from wind direction after 2.5, 5, and 10 m of flight were 19.4°, 18.6°, and 18.0°, respectively. These deviations were less than 90° in all instances; far from 180°, the expected mean associated with random flight orientations. Therefore, if experimental releases are conducted with wind direction perpendicular to the direction of the target habitat patch (as would be recommended), the proportion of butterflies failing to detect habitat patches, but still orienting towards them, will be lower than what is predicted by random flight orientations. These results suggest that the random flight null assumption is biased towards overestimating null proportions of butterflies successfully orienting towards adjacent habitat patches, and is therefore inappropriate for determining thresholds of perceptual range.

Qualitative observations of flight behavior support this conclusion. In all instances of success navigation, we observed a surprisingly punctuated shift in flight behavior, from a 'fluttering' flight averaging with the wind direction, to a 'directed' flight towards the target island. We interpret this change in flight behavior as meaningful perception of, and reorientation towards, the target island based on several observations. Almost all individuals that did not successfully navigate to the target island vanished from sight following the wind direction. We did not observe a single instance wherein an individual exhibited a directed flight toward the target island, but failed to successfully navigate to it. Furthermore, there were very few instances (three flashed *S. cybele*) wherein an individual maintained a fluttering flight in the direction of the target island, until it arrived at the island's shore, without adopting a directed flight. We therefore find it reasonable to conclude that: 1) most, if not all, instances of failed to navigation to the target island represented failure to detect the target island and 2) most instances of successful navigation to the target island represented meaningful detection of the target island. It is also reasonable to infer that unsuccessful and successful butterflies were similarly searching for suitable habitat, and that butterflies drifting with the wind direction were not simply exhibiting an escape response. While flight paths of successful butterflies were significantly more tortuous than unsuccessful butterflies (Model 4), this difference was caused by the consistent reorientation of successful butterflies from wind direction to island direction following detection of the target island (Models 5 and 6). Flight patterns of successful and unsuccessful butterflies were generally indecipherable before successful butterflies detected and reoriented towards the target island.

While the probability of *S. cybele* and *S. atlantis* successfully detecting and navigating to the target island significantly decreased with increasing release distance, no obvious distance threshold was observed for either species. We see little reason to infer that single distance measures (i.e., thresholds) of perceptual range are ecological meaningful a priori. While ommatidial structure suggests the existence of single object thresholds (sensu Rutowski 2003), the probability of a dispersing butterfly detecting a nearby habitat patch is subject to a plethora of factors unique to landscapes, individuals, and environmental conditions. Indeed, the level of visual contrast between habitat patches and the matrix (sensu Rutowski 2003),

the evolutionary history of individuals (e.g., Merckx and Van Dyck 2007), the perceived suitability of the matrix (e.g., Nowicki et al. 2014), and the wind speed and direction (this study) represent but a few factors that warrant continued investigation. Accounting for factors unique to landscapes, individuals, and environmental conditions (as in multiple logistic regression), perceptual range may be best viewed as a continuum of conditional probabilities, reflecting the likelihood that butterflies will detect habitat patches across a range of distances, rather than a single distance measure per se. This approach has the added benefit of permitting quantitative comparisons of probabilities of detecting habitat patches at distances below perceptual range thresholds, should they be found to exist in future research. To avoid confusion of terms in the literature, we suggest this concept may be referred to as 'targeting ability'.

Targeting Ability and Habitat Fragmentation

In contrast with single distance measures of perceptual range, the concept of targeting ability does not evoke punctuated distinctions between apparent and functional fragmentation (sensu Schtickzelle et al. 2007, Dover and Settele 2009). We find there is little evidence to suggest that this dichotomous distinction, predicated on thresholds of patch isolation and perceptual range, is ecologically meaningful. For example, the degree of asynchrony between subpopulation dynamics in metapopulations have been shown, both theoretically and empirically, to vary continuously with patch isolation (review in Hanski 1999). Furthermore, within fragmented landscapes, dispersal ranges of butterflies are commonly observed as 10–1,000-fold greater than the greatest distance estimates of perceptual range (e.g., 37 km for the cranberry fritillary [*Boloria aquilonaris* (Stichel, 1908) (Lepidoptera: Nymphalidae), Baguette 2003]; see Introduction for review of perceptual range estimates). During dispersal events, the probability of a butterflies encountering habitat patches is well-approximated by a variety of functions, such as negative exponential or inverse power, where increasing patch isolation has continuous, rather than threshold, effects on the probability of patch colonization (Hanski et al. 2000, Baguette 2003, Nowicki et al. 2014). Even when interpatch distances and movements do not exceed estimated perceptual range thresholds (i.e., short-range dispersal), organisms are still likely to experience increased mortality risk or deferred costs when moving between patches. Thus, punctuated distinctions between apparent and functional fragmentation may bear little resemblance to ecological patterns and processes on many fragmented landscapes.

Of greater ecological relevance, Baguette and Van Dyck (2007) advance a conceptual distinction between different perspectives of landscape connectivity, [structural' and 'functional', without emphasizing specific thresholds of patch isolation in relation to perceptual range. Within this framework, structural connectivity addresses the spatial configuration of habitat patches and landscape elements, such as the vicinity and presence of barriers, while functional connectivity addresses how landscape structure affects behaviors of dispersing individuals. In other words, functional connectivity contributes to the concept of structural connectivity by accounting for perceptual grain; the smallest spatial scale at which organisms perceive landscape heterogeneity (Wiens 1989). Perceptual grain is most often inferred via estimates of single distance (threshold) measures of perceptual range (Baguette and Van Dyck 2007). Including addition facets of habitat detection associated with the concept of targeting ability (e.g., factors unique to landscapes, individuals, and environmental conditions) may further the instructive power of the functional connectivity heuristic.

Targeting Ability of *S. cybele* and *S. atlantis*

Despite considerable overlap in their evolutionary and life histories (Hall et al. 2014, Acorn and Sheldon 2017), a significant difference in targeting ability was observed between *S. cybele* and *S. atlantis*. Overall, *S. cybele* were 2.48 times more likely to successfully navigate to the target island than *S. atlantis*. A noted difference in compound eye structure between the two species is color, with compound eyes of live *S. cybele* and *S. atlantis* appearing brown and gray, respectively (Acorn and Sheldon 2017). This difference may be attributed to variation in the composition of screening pigments, which filter light passing both onto photoreceptive rhodopsins and between separate ommatidia (Stavenga 2002). Red screening pigments of the Japanese yellow swallowtail butterfly (*Papilio xuthus* Linnaeus, 1767 (Lepidoptera: Papilionidae)) are inferred to act as short-wavelength absorbance filters, facilitating long-wave sensitivity of rhabdomeres (Arikawa et al. 1999). Via this mechanism, dark-orange screening pigments of the monarch butterfly (*Danaus plexippus* (Linnaeus, 1758) (Lepidoptera: Nymphalidae)) have been shown to contribute to color discrimination in the long-wavelength range (Blackiston et al. 2011). Together, these studies suggest a link between screening pigment composition visual sensitivity under various light conditions. However, additional research will be required to resolve whether interspecific variation in screening pigment composition among *Speyeria* species relates to variation in visual targeting ability.

Of greater interest to this study are relationships between interspecific variation in targeting ability and functional traits known to relate to dispersal, such as wingspan and estimates of mobility (Burke et al. 2011, Stevens et al. 2012). Wingspans of *S. cybele* and *S. atlantis* in Ontario have been measured at 70–100 and 55–70 mm, respectively (Acorn and Sheldon 2017). Burke et al. (2011) have estimated the mobility of *S. cybele* and *S. atlantis* at 7.10 and 7.00, respectively, using a qualitative index (based on expert opinion) ranging from 0 to 10. In accordance with positive interspecific relationships between wingspan, mobility, and dispersal ability of butterflies (e.g., Stevens et al. 2012), the larger and more mobile of the two species, *S. cybele*, had significantly greater targeting ability than did the smaller and less mobile of the two species, *S. atlantis*. In the context of the functional connectivity heuristic (sensu Baguette and Van Dyck 2007), interisland movements and dispersal are likely to be less costly, both in terms of mortality risk and deferred costs, for *S. cybele* than *S. atlantis*. *Speyeria cybele* may therefore have greater a greater propensity and ability to navigate fragmented landscapes than *S. atlantis*. However, this inference is drawn from a single comparison of two congeneric species. More comprehensive studies, addressing disparity in targeting abilities across a greater number of species, is required to appropriately evaluate the hypothesis that targeting ability is a practical measure of the degree to which organisms perceive landscapes as fragmented. It is also worth noting that this study was completed in a landscape of extreme habitat-matrix contrast. Comparisons of related studies addressing terrestrial landscapes of greater complexity would be valuable for understanding how organisms perceive fragmented landscapes with lower habitat-matrix contrast (e.g., for a comparisons of diversity patterns on a true-island archipelago and an anthropogenically fragmented landscape, see Mendenhall et al. 2014; or butterfly movement through different scales of linear forest fragmentation, see Riva et al. 2018).

Determinants of Targeting Ability

Given the prominence of morphological traits associated visual senses, butterflies have long been hypothesized, and even assumed, to rely primarily on vision to detect and navigate to habitat patches during dispersal movements (Silberglied 1984, Rutowski 2003, Turlure et al. 2016). However, to the best of our knowledge, this hypothesis has evaded explicit empirical investigation using experimental techniques. Thus, an interesting finding of this study is that repeated exposure to an intense flash significantly reduced the ability of both *S. cybele* and *S. atlantis* to detect and navigate to suitable habitat from a range of distances. This effect of flashing was substantial, with flashed individuals 30.13 times less likely to successfully navigate to the target island than unflashed individuals. The proportion of flashed butterflies successfully navigating to the target island was near zero or zero at all distances. Given these findings, we infer that visual senses of *S. cybele* and *S. atlantis* play a primary role in navigating fragmented landscapes when visual habitat-matrix contrast is high. However, we cannot rule out that olfaction may be used synergistically with vision, as demonstrated for long-range detection of nectar resources (Cardé and Willis 2008) and identification of larval host plants (Rausher 1981, Papaj, 1986, Garlick 2007, Kinoshita et al. 2015). Notwithstanding, results of our study support the long-held assumption that visual senses are a primary means by which the butterflies detect and navigate to patches of suitable habitat while moving through matrices of unsuitable habitat.

In light of this conclusion, it is both unexpected and interesting that angular subtense of the target island did not explain more variation in navigation success than distance per se. If visual senses do indeed account for long-range habitat detection in butterflies, the apparent sizes of habitat patches (angular subtense) should relate to their probability detection (i.e., single object thresholds; sensu Rutowski 2003). However, GLMs indicated that probability of successful navigation was not significantly related to angular subtense, despite the fact that angular subtense was strongly correlated with release distance. Taken at face value, this finding suggests that: 1) there are intrinsic effects of distance per se on butterflies' ability to detect habitat patches and 2) perceptual range and targeting ability may not vary with patch size. However, this latter conclusion contrasts with the common and reasonable assumption that patches or islands of larger areas present larger dispersal targets (sensu Wilson and MacArthur 1967, Hanski 1999). It is worth noting here that the target island was approximately circular in shape, meaning angular subtense did not vary substantially independent of release distance in this study. We therefore question whether the conclusion, that perceptual range and targeting ability may not vary with patch size, is meaningful. Relationships between patch size and patch detectability, and their relevance to the dispersal process, require further investigation.

A superior assessment of relationships between patch size and patch detectability would empirically determine, across a range of release distances, variation in the probability of butterflies detecting habitat patches that vary substantially in area and thus angular subtense. Including habitat patches that also vary in habitat height would permit two-dimensional estimations of angular subtense, deepening inferences that may be drawn. Measures should be taken to quantify relative levels of visual contrast between habitat patches and their immediate surroundings if patch or matrix compositions are heterogeneous. As butterflies are inferred to have color vision (Silberglied 1984, Kinoshita 1999, Arikawa 2003, Blackiston et al. 2011), quantifying visual contrast across a variety of wavelengths may permit decoupling of specific visual ques used by butterflies to detect habitat or resource patches in heterogeneous landscapes.

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