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Effects of fragmentation per se on slug movement

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ABSTRACT

To predict the effects of habitat alterations on animal populations we need insight into how the habitat configuration influences local scale movements. This relationship may be particularly important for effective management of pest species. We tracked 80 PIT-tagged Spanish slugs (*Arion vulgaris*) in 16 × 16 m arenas with manipulated habitat fragmentation. The arenas had habitat patches consisting of high grass residing within a matrix of short grass, and the arenas with a high degree of fragmentation had 12 large (2 × 2 m), 13 medium-sized (1 × 1 m) and 12 small (0.5 × 0.5 m) patches, whereas the arenas with low fragmentation had four 4 × 4 m patches, resulting in equal amounts of total habitat patch area in the two treatments. The measured mean distance moved per day was 3.8 m, and between 0 and 25% of the slugs left the arenas each day. Fragmentation treatment had no effect on these two measurements. In the treatment with patches of different sizes, slugs distributed themselves among the patch size classes according to the total amount of habitat area for each habitat patch class, whereas patch edge did not explain the distribution pattern. All in all, fragmentation per se seems to play a minor role in the local movement and distribution of Spanish slugs.

1. Introduction

The composition and configuration of habitats of different quality may have important effects on the growth, spread and reproduction of organisms (Turner and Gardner, 2015). An understanding of how the quality, configuration and connectedness of different habitats influence movement of organisms is fundamental for predicting the effects of anthropogenic habitat alterations on population dynamics (e.g., Collinge, 2000; Moorcroft, 2012). Investigating these effects may be particularly important for the development of effective measures to prevent damage from non-native pest species (With, 2002) by, for instance, designing and managing agricultural and urban areas to influence movement and dispersal rates (e.g., With et al., 2002; Thiele et al., 2008; Klinger et al., 2019).

Habitat fragmentation often leads to a decrease in habitat area, an increase in the number of habitat patches, a decrease in the average size of remaining habitat patches and an increase in patch isolation (Fahrig, 2003, 2017; With, 2019). These changes in patch number and size increase the amount and density of edges, which are the transitions between adjoining habitats or habitat and matrix (Murcia, 1995). Most researchers have found negative effects of fragmentation on ecological patterns and processes, such as diversity, demography and movement (Fahrig, 2003). The majority of these plot-scale studies measured solely the effects of the inevitable habitat loss resulting from fragmentation (Fahrig, 2003), whereas experiments are needed to differentiate between the effects of habitat amount and fragmentation per se (Fahrig, 2017). Summarizing the available studies on fragmentation per se, Fahrig (2017) showed that 76% of significant responses to habitat fragmentation per se, i.e. independent of habitat amount, were positive. This compilation also showed that there were only 11 published papers analyzing the movement of species, of which the majority focused on either mammals (5) or insects (4), whereas data from reptiles and birds were reported in only one paper each. Notably, none of these studies focused on gastropods, an ecologically important and diverse group. For this group, foraging, sheltering, egg-laying and overwintering habitats are often spatially separated, and local movements between these habitats are therefore a crucial part of their ecology (Cameron, 2016). To mitigate crop damage from gastropod pests and to develop conservation programs for threatened species, knowledge of their movement ecology is essential.

Animals move to find foraging and mating opportunities, to avoid competition and predation and to find shelter against adverse physical environmental conditions. Movement between habitat patches is influenced by several factors, such as different qualities of the patches and

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the matrix, distances between patches, patch numbers and sizes and the amount of edge (e.g., Andreassen and Ims, 2001; Goodwin and Fahrig, 2002; With et al., 2002; Grez et al., 2005). The impact of these factors on the behavioral decisions made by individuals forms the link between the habitat configuration and the animals' ecology. Furthermore, the relative importance of different resources and the possibility to move in the matrix may change with time of day. These dynamics result in diel lifestyles, in which movement and foraging are either a diurnal or nocturnal activity. Particularly if shelter and food resources are spatially separated, animals must tradeoff movements for finding food and securing shelter to avoid exposure while resting.

Terrestrial gastropods play an important and diverse functional role in ecological communities, comprising grazers and decomposers (van Grunsven et al., 2018), predators (Barker and Efford, 2004; Miczajka et al., 2019), prey (Zając et al., 2017) as well as vectors for dispersal of other invertebrates and seeds (Türke et al., 2010, 2018). Slugs, in particular, often receive attention as pest species (Cowie and Robinson, 2003), and in northern Europe for example, the Spanish slug (*Arion vulgaris*) has become an important invasive species that causes problems in gardens and agriculture (Frank, 1998). As for other slug species, movement is central to the ecology of the Spanish slug (Nyqvist et al., 2020). Although long distance invasion is typically driven by accidental egg and juvenile transmission in the trade of soil and plants (Zając et al., 2017), slug movement patterns may be important for understanding mechanisms that affect local dispersal, as well as directed daily or seasonal migrations between habitats (Nyqvist et al., 2020). Describing these movement patterns may also be a key factor to facilitate the development of measures to reduce crop damage caused by slugs (Watz and Nyqvist, 2021). During dry summer periods, Spanish slugs typically migrate between moist daytime shelters and nearby nocturnal feeding habitats (Grimm et al., 2000), and on a seasonal basis, adults move to egg-laying habitats and juvenile slugs move to find suitable places for overwintering (Kozlowski and Kozlowski, 2011).

Habitat affects the movement patterns of terrestrial gastropods. For example, the Oregon forest snail (*Allogona townsendiana*) displays smaller home ranges in habitats with high than in habitats with low availability of stinging nettles that constitute both a food resource and offer suitable sheltering habitat (Edworthy et al., 2012). Rock-dwelling land snails (*Chondrina clienta)* disperse longer distances in homogenous pavement and rock walls compared to more complex stone piles and stone walls (Baur and Baur, 1995). Spanish slugs move longer distances and have larger home ranges in a relatively homogenous forest compared to garden habitat with an uneven distribution of shelters and feeding habitats (Nyqvist et al., 2020). Field experiments with manipulation of the level of habitat fragmentation are lacking. Here, we used telemetry to investigate the movement of Spanish slugs in experimental arenas in either high or low habitat fragmentation per se, i.e. having the same total amount of habitat per arena. The main resource in the habitat patches was daytime shelter, a non-consumable resource. We predicted that slugs would move longer distances in the arenas with high than low fragmentation. We base this prediction on the results of the aforementioned correlative studies of terrestrial gastropod movement in relation to availability of sheltered habitat (Baur and Baur, 1995; Edworthy et al., 2012). Also, many small, dispersed patches of daytime sheltering habitat may increase the overall area that can be used for nocturnal foraging, because the chance of a nearby habitat patch will be higher when the slugs need to seek daytime shelter (Nyqvist et al., 2020). Moreover, we tested if habitat patch size related to patch use and movements within and out of patches and the arenas.

2. Material and methods

2.1. Site description

The study was carried out in August 2020 in a 0.4 ha grass field in the town of Kristinehamn, Sweden (WGS84: 59.330, 14.087). We selected four 16 × 16 m experimental arenas placed at least 12 m from each other (Fig. 1). Oak trees (*Quercus robur*) shaded the experimental arenas to a relatively low extent, and mean canopy openness ± SD measured using a fisheye objective at 16 positions (four in each arena) was 88.2 ± 12.6% (Table 1). In the experimental arenas, we mowed the grass to create patterns with quadratic high grass habitat patches of different sizes residing within a matrix of short grass (Fig. 1). We assumed that the patches with high grass constituted a habitat with higher quality during daytime (e.g. offering shade and moisture) than the short grass matrix. Outside of the test arenas, we mowed the grass in the same way as for the matrix inside the arenas, making the test arenas islands of high grass patterns (Fig. 1). During the study period, mean maximum and mean average grass height ±SD inside 48 randomly selected high grass patches were 19.7 ± 5.5 and 14.8 ± 4.1 cm, respectively. The corresponding values for 16 positions within the short grass matrix were 6.8 ± 2.1 and 4.2 ± 1.6 cm (Table 1). Mean relative air humidity and temperature (measured each day 1 m above the ground at midday) ± SD during this period were 49.3 ± 11.9% and 25.2 ± 3.0 °C.

The pattern of patches in two of the experimental arenas were configured so that the arenas each contained 12 large (2 × 2 m; total = 48 m^2), 13 medium (1 × 1 m total = 13 m^2) and 12 small (0.5 × 0.5 m total = 3 m^2) evenly distributed patches (a total of 37 patches = 64 m^2). The pattern of the two other arenas were configured to have fewer and larger patches (four 4 × 4 m patches total = 64 m^2). Total patch area was therefore equal in all four experimental arenas regardless of configuration (Fig. 1). The arenas with many patches of different sizes (0.25, 1 and 4 m^2) and the arenas with few patches of equal and larger size (16 m^2) are henceforth referred to as having a high and low fragmentation treatment, respectively.

2.2. Slugs

Slugs (*Arion vulgaris*) were collected at the edge of a nearby, forested area. We tagged slugs on 7 and 9 August 2020 with 12 mm passive integrated transponders (PIT; Oregon RFID, Portland, US). The slugs were sedated for 5–15 min with MS-222 (tricaine methanesulfonate) dissolved in water at a concentration of 300 mg L^{-1}, and we inserted the PIT tags through a small incision made at the middle of the foot (Nyqvist et al., 2020). We used 80 tagged slugs in the experiment with a mean body mass (±SD) of 8.2 ± 2.5 g.

2.3. Data collection

Into each test arena, we released 20 randomly selected slugs on 10 August 2020 at 22:00. From 11 to 18 August, we tracked the slugs daily starting at noon (12:00 ± 1 h). We carefully searched the four experimental arenas and their immediate surroundings (a 5 m strip outside of the arenas), followed by a quicker search of the rest of the field and its surroundings. A tracking survey took c. 2 h. The antenna's circular coil (diameter = 50 cm) has a "blind spot" in its centrum, which often (depending on tag orientation and distance to other tags) permits its users to locate tags with precision down to 10 cm (Watz et al., 2016). We used this blind-spot method to locate the position of each detected slug, and we assigned it to the nearest 0.5 m orthogonal coordinate on a map. When slugs were located in the experimental arenas, we noted if the slug was found outside or inside of a patch with high grass and, in the latter case, the size of the patch. We also noted if a slug had left its patch for another patch, to the matrix inside the arenas or to the area outside of the arenas.

2.4. Data analysis

Data from slugs found dead during or after the study were included as long as the slugs were observed moving >1 m in the experimental arenas. Data from slugs that left the arenas and were not recaptured or found dead were included, as we assumed that they were not removed

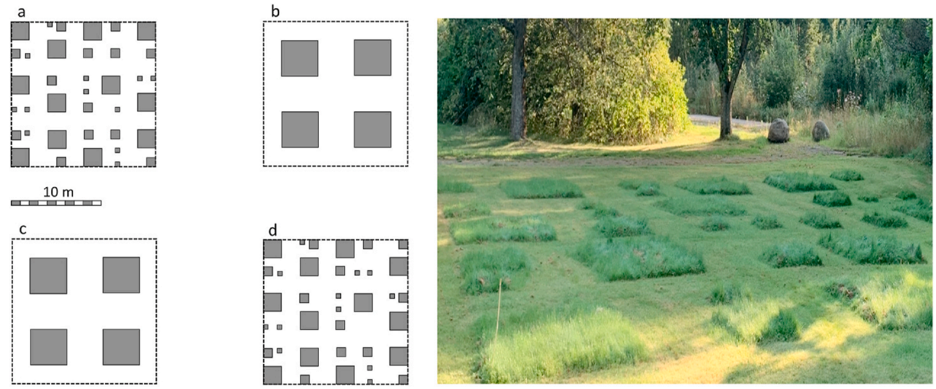

Fig. 1. To the left, a schematic drawing of the layout and placement of the experimental arenas (a–d) demarcated by dashed lines, with habitat patches (grey squares) consisting of high grass placed in a matrix (white background) consisting of short grass. Experimental arenas a and d had high and b and c low degree of fragmentation. To the right, a photograph of experimental arena d.

Table 1
Description of the four experimental arenas (a – d) with their respective habitat treatment (H = high fragmentation; L = low fragmentation), mean site openness (i.e. lack of canopy cover) and matrix and patch (sizes: 4 × 4, 2 × 2, 1 × 1 m, 0.5 × 0.5 m) mean maximum and mean average grass height.

Arena	Treatment	Site openness ± SD (%)	Maximum/average grass height ± SD (cm)				
			Matrix	*4 × 4 m*	*2 × 2 m*	1 × 1 m	0.5 × 0.5 m
a	H	98.6 ± 0.7	5.5 ± 1.3/ 4.8 ± 2.9	–	20.3 ± 9.3/ 13.8 ± 5.0	15.3 ± 2.1/ 12.5 ± 1.0	16.8 ± 4.5/ 12.3 ± 4.9
b	L	99.6 ± 0.2	6.5 ± 2.4/ 4.3 ± 1.3	17.3 ± 4.8/ 14.8 ± 6.9	–	–	–
c	L	75.1 ± 7.7	5.8 ± 1.7/ 3.3 ± 0.5	20.5 ± 3.7/ 14.5 ± 1.3	–	–	–
d	H	79.6 ± 11.5	9.5 ± 0.5/ 4.5 ± 0.6	–	22.8 ± 4.3/ 17.3 ± 3.3	23.8 ± 5.7/ 17.5 ± 4.7	21.3 ± 5.3/ 16.3 ± 1.7

from the area by external forces (local predation pressure is considered low), but instead migrated away and thus were alive when we had detected them.

Once a slug was found outside of the experimental arena in which it had been released, the slug's positions recorded in subsequent surveys were not used in the analyses. Hence, the last position data included in the analyses from a slug either originated from the first time the slug was located outside of its experimental arena or, for slugs that did not leave the arenas, the last time that it was detected. When a slug was detected during two consecutive tracking surveys, we calculated the movement as the shortest path between the two positions. This estimation of distance moved assumes that slugs travel in a straight line, which is in most cases not true. Therefore, the distances we report here are underestimated.

To assess potential differences in (1) distance moved between the arenas with high and low fragmentation, we used a linear mixed model with fragmentation treatment and arena ID nested within treatment as fixed factors. To account for the repeated measures on individual slugs, we included slug ID as a random factor with the covariance matrix specified as first-order autoregressive. To test if the fragmentation treatment affected (2) the probability to leave the experimental arena, we used a generalized linear mixed model with a binomial error distribution, also with fragmentation treatment and arena ID nested within fragmentation treatment as fixed factors and slug ID as a random factor (first-order autoregressive).

We tested if the size of the patch from which a slug started a movement affected (3) the probability to leave the arena and (4) the probability to leave the patch. For these analyses we used generalized mixed linear models (binomial error distribution), with patch size as a fixed factor and slug ID as a random factor (first-order autoregressive). Moreover, we tested if (5) moved distance inside and (6) out from a patch was affected by patch size using linear mixed models with patch size as a fixed and slug ID as a random factor (first-order autoregressive).

We tested whether or not slugs preferred the patches of high grass to the matrix as daytime habitat. For each slug detected within an experimental arena at least twice during the study, we calculated the proportion of detections within patches (vs the matrix). Using a one-sample Wilcoxon signed rank test with slug individuals as replicates, we (7) compared these proportions to the expected median value if the slugs distributed themselves randomly within the arenas. Similarly, for slugs detected within patches in the arenas with high fragmentation, we used separate one-sample Wilcoxon signed rank tests for each patch size class to analyze (8) whether slugs used the respective patch size class to the same proportion that would be expected if total patch class area or total patch edge (Lang and Blaschke, 2007), respectively, played a major role.

3. Results

During or after the study, 24% of the slugs were found dead, and 12.5% left the arenas and were not recaptured or found dead. A total of 241 locations were detected from 67 live slugs within the arenas. The number of slugs and detections were similar among the arenas (arenas with high fragmentation: 18 and 17 slugs, 69 and 57 locations; low fragmentation: 16 and 16 slugs, 53 and 62 locations). During the study, 194 movements were recorded (mean distance moved $day^{-1} \pm SE = 3.8 \pm 0.3$ m). Of these, 27 movements resulted in the slug leaving its experimental arena, and the leaving rate varied among days between 0 and 25% of the detected slugs. Movements that started from inside a patch (n = 182) resulted in 111 movements inside the same patch and 71 movements in which the slug left its patch. Each day during the study, between 25 and 56% of the slugs that started from a patch left this patch each day and was subsequently tracked outside that patch (in another patch, in the matrix or outside the arena).

There was no difference in distance moved per day between the fragmentation treatments ($F_{1,29.5} = 0.05$, p = 0.83; Fig. 2) or the arenas nested within treatment ($F_{2,29.5} = 0.02$, p = 0.98). Likewise, these two

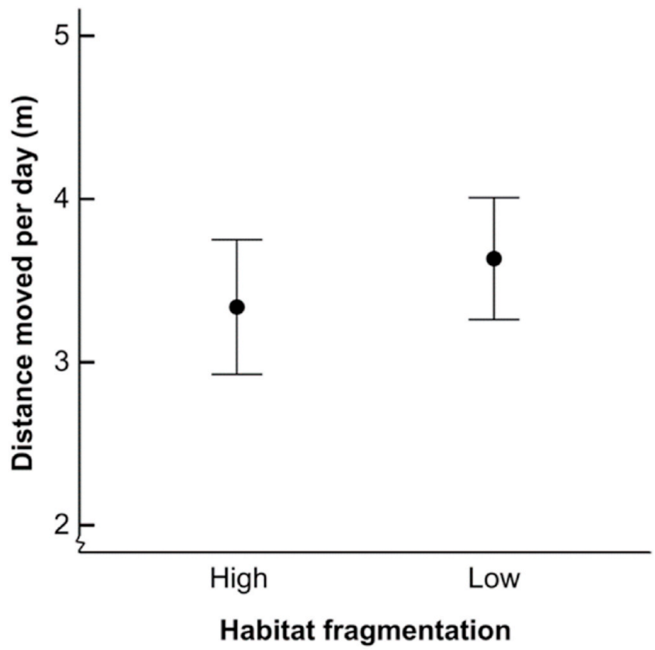

Fig. 2. Mean distance moved per day (±SE) by Spanish slugs in arenas with high and low habitat fragmentation.

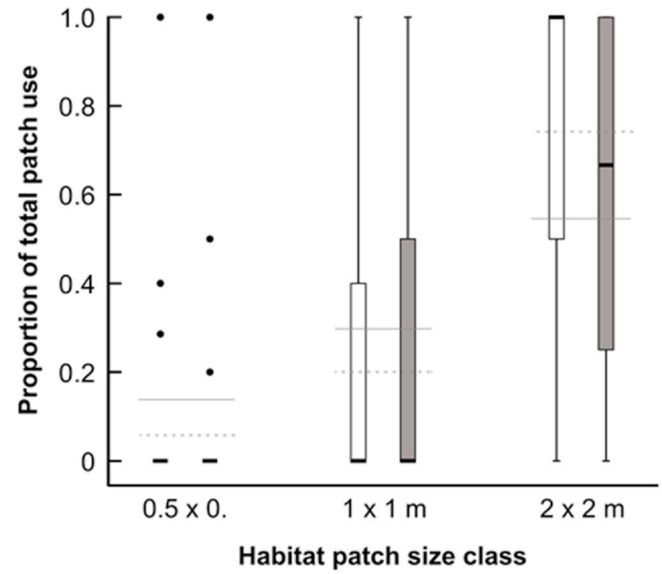

Fig. 3. Boxplot of patch size class use by Spanish slugs for two test arenas (arena a – white bars to the left in each pair; arena d – grey bars to the right). Grey thin dotted lines represent the expected values if slugs selected patches according to total area for respective patch size class. Grey thin solid lines represent the expected values according to total amount of edge for respective patch size class.

parameters had no effect on the probability to leave the experimental arenas ($F_{1,190} = 0.05$, $p = 0.83$ and $F_{2,190} = 0.02$, $p = 0.98$; Fig. 1). The size of the patch that a slug resided in had no effect on the probability of leaving the experimental arena ($F_{3,178} = 1.80$, $p = 0.15$) or leaving the patch ($F_{3,178} = 2.23$, $p = 0.09$). For movements inside patches, there was a positive relationship between patch size and the distance moved ($F_{2,35.4} = 18.89$, $p < 0.001$), and inside 4 × 4 m patches, slugs moved (mean ± SE) 1.5 ± 0.1 m whereas slugs in the 2 × 2 and 1 × 1 m patches m patches moved 0.7 ± 0.1 and 0.3 ± 0.1 m, respectively. In the smallest patches (0.5 × 0.5 m), our method did not have enough resolution to detect movements. For slugs leaving their patches, there was no such relationship between patch size and distance moved ($F_{3,47.9} = 1.40$, $p = 0.25$) and these movements were 7.1 ± 0.5 m long.

For slugs detected at least twice within the experimental arenas (n = 46), mean proportion of patch use (±SE) across all four arenas was 0.94 (±0.02). The median proportion of patch use deviated from the expected value (0.25, i.e. the proportion of total patch area within each experimental arena) if the slugs had distributed themselves randomly (for arenas a – d: Z = 3.32, 3.30, 2.91 and 3.16, $p < 0.01$). In the arenas with high fragmentation (with patches of different sizes), 23 slugs were detected at least twice. The mean proportion of patch use (±SE) for small (0.5 × 0.5 m), medium (1 × 1 m) and large (2 × 2 m) patches, respectively, were 0.10 (±0.05), 0.23 (±0.06) and 0.65 (±0.07). If slugs distributed themselves among patch size classes according to total patch size class area and amount of edge, respectively, the expected proportions would be [0.05, 0.20 and 0.75] and [0.14, 0.30 and 0.56]. The observed median proportion did not significantly differ from what would be expected according to *total patch class area* for both arenas (arena a and d: n = 13 and 10, $Z_{0.5\times0.5} = 0.70$ and 0.92, $p_{0.5\times0.5} = 0.48$ and 0.36, $Z_{1\times1} = 0.82$ and 0.87, $p_{1\times1} = 0.41$ and 0.38, $Z_{2\times2} = 0.11$ and 1.29, $p_{2\times2} = 0.92$ and 0.20; Fig. 3). Conversely, the observed median for the use of medium-sizes patches differed from the expected value according to *amount of edge*, albeit only for one of the arenas (arena a and d: n = 13 and 10, $Z_{0.5\times0.5} = 0.70$ and 1.78, $p_{0.5\times0.5} = 0.48$ and 0.08, $Z_{2\times2} = 2.03$ and 0.05, $p_{1\times1} = 0.04$ and 0.96, $Z_{large} = 1.45$ and 0.46 $p_{2\times2} = 0.15$ and 0.65; Fig. 3).

4. Discussion

Slugs showed a clear preference for the high grass habitat within the experimental arenas during the tracking occasions. Surface area, rather than the amount of edge, seemed to better relate to the distribution of slugs among different-sized high grass patches. The fragmentation treatment did not affect the probability of emigration from the arenas, and slugs moved similar distances between tracking occasions in the arenas with high and low fragmentation. These results on movement did not support our predictions regarding the effects of fragmentation per se. Distances moved, however, were likely underestimated in our study, and higher temporal resolution tracking data may provide different results. Within arenas with different-sized patches (high fragmentation treatment), patch size affected the probability to leave the patch, but not the arena. Slugs moved longer within large than within small patches. This result is unsurprising and may be an artifact of the experimental design because of the limited resolution of the tracking procedure. Once leaving a patch, patch size did not affect the distance moved.

Previous studies describing the effects of fragmentation per se on invertebrate movement have focused exclusively on insects. For instance, field experiments on predatory beetles using arenas with manipulated fragmentation have both shown positive (*Coleomegilla maculate*, With et al., 2002) and no effects (*Eriopis connexa*, Grez et al., 2005) of fragmentation on movement. In the latter study, movement was negatively related to interpatch distance, but no effects of fragmentation on the probability to stay within the arenas was found. In a correlative study on meadow brown butterflies (*Maniola jurtina*), the same effect of interpatch distance was shown, whereas other variables had no major effect (Ouin et al., 2008). In experiments based on combined simulation and empirical data from goldenrod beetle movement (*Trirhabda borealis*), Goodwin and Fahrig (2002) came to the similar conclusion that increasing the interpatch distance reduced landscape connectivity and that the effect of fragmentation per se was less important. In contrast to many other studies, ours was designed to test the fragmentation of habitat with a non-consumable resource (daytime shelter). Nevertheless, the lack of effects of fragmentation per se in our study seems to corroborate these findings on other invertebrates.

Within the treatment with high fragmentation, the daytime locations of individuals were likely distributed among the patches according to their relative area, and less so according to their relative amount of edge. These results indicate that edges may play a minor role in daytime habitat selection, especially when the habitat does not offer improved feeding opportunities (Rollo, 1983). Responses to edges may be idiosyncratic, depending on species-specific edge sensitivity (Ries and Sisk, 2010) and the characteristics and history of habitat edges (Magura et al., 2017). Our results suggest that the Spanish slug as a generalist shows a neutral edge response in relation to its movement patterns because distances moved did not vary between the arenas with manipulated degrees of fragmentation. Although the species shows diurnal differences in resource needs and its maneuverability probably varies between habitat patches and matrix, the mobility of the species is apparently large enough to allow movement between habitat and matrix in the experimental arenas that we provided.

We tracked the position of the slugs during daytime, and we therefore primarily studied movements between daytime sheltering positions. A slug tracked in the same patch at two consecutive tracking occasions may have been resident in the patch, but may also have ventured out of the patch and returned before the next day. Slugs are primarily nocturnally active and move out from their shelters during the dark and humid hours (South, 1992). Although homing to daytime shelter occurs in terrestrial gastropods (Gelperin, 1974; Tomiyama, 1992), it has not yet been observed in Spanish slugs (Nyqvist et al., 2020).

The quality of the high grass habitat is difficult to estimate. The daytime tracking surveys showed that the slugs had a strong preference for the high over the short grass. Hence, the high grass likely constituted a suitable, relatively humid, sheltering habitat. The high grass also potentially offered some food resources in the form of living and dead organic material, but perhaps not enough to keep the slugs from venturing out to find better feeding opportunities. In our experiment, there was no difference in emigration from the arenas depending on habitat fragmentation, and patch size did not affect the probability to leave the patch or distance moved from patches when doing so. In a garden, this would mean that the distribution of a given area of high grass habitat (or other suitable shelter) should be of limited importance to the slugs' consumption of horticultural crops, given that they are within excursion range.

Large arionid slugs are relatively easy to tag with PIT, can be tracked with mobile and stationary antennas and have limited movement ranges (Grimm and Paill, 2001; Nyqvist et al., 2020). Using telemetry potentially increases the amount of movement data that can be collected compared to mark-recapture-based designs, and telemetry detections do not interfere with the animals' behavior, as can be the case when using traps. With little effort, a mosaic of high and low grass can be created and replicated for slugs to move in, and this system has potential to be valuable for answering a wide range of research questions related to movement in the field of behavioral landscape ecology. For example, further research on habitat configuration such as effects of patch shape and placement, barriers and matrix characteristics can be tested. Moreover, the interaction between the configuration and both intrinsic (e.g. energetic state, degree of maturation and animal personality) and extrinsic factors (e.g. predation, parasites, competitors and physical conditions such as temperature) may be explored (Cloyed and Dell, 2019). From a horticultural perspective, incorporating high value crops that could constitute a preferred nocturnal feeding habitat may give valuable knowledge for designing pest control measures.

5. Conclusion

The relationship between habitat and behavioral ecology is crucial to understand for managing pest species. Although the Spanish slug causes considerable economic damage to horticultural and agricultural crops (Kozlowski and Kozlowski, 2011), as well as pose a threat to urban biodiversity (Zając et al., 2017), our knowledge is relatively limited about how the habitat configuration influences local dispersal and population dynamics. We have taken a first step to shed light on this question by showing that habitat fragmentation per se does not seem to affect slug movement.

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Conflicts of interest/Competing interests

None.

Ethics approval

Not applicable.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Code availability

Not applicable.

Authors' contributions

JW and LE conceived the idea for the study. JW, LE and DN designed the study. JW collected and analyzed the data. JW, LE and DN wrote the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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