Bats as indicators of habitat connectivity in urban environments

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‘We need to learn how to work with nature rather than against it’
- David Attenborough

Abstract

Human disturbances to natural environments have been an increasing issue since the industrial revolution when the human population started to grow faster than ever before. Habitats have been extensively lost, followed by severe consequences on biodiversity. Bats are one order that has suffered from population declines caused by habitat loss - either from complete loss, or lost accessibility caused by fragmentation. The forest living bat species are particularly affected by forest fragmentation because they avoid crossing open ground. This may be because of predator avoidance, which also seems to be the reason they avoid light. This study examines whether connectivity facilitates movement between habitats in the landscape for the forest dwelling *Myotis* species. Bat activity was recorded with automatic ultrasound detectors in habitat elements with different levels of isolation (isolated islands, connected islands, corridors and continuous forest as controls) in Tierp, Sweden, during the month of July 2021. In general, the occurrence of *Myotis* on islands was not different from mainland, and there was no correlation between occurrence on isolated islands and size, distance to mainland, or distance to nearest habitat. However, the occurrence on isolated islands was related to the date of observation. This could be explained by the light summer nights of northern Europe in June and beginning of July. When observations later in July were excluded, occurrence on isolated islands was related to island size, thus when nights became darker bats dispersed to more isolated habitats. Light seems to enhance the isolation effect and be a bigger impediment for habitat use than fragmentation alone.

Keywords: Bats, Sweden, light, fragmentation, connectivity, urban, Myotis, Myotis brandtii

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1. Introduction

Anthropogenic alterations in natural environments have degraded ecosystems on a large scale ever since the industrial revolution at which time the human population started to expand faster than ever before. One fourth of the Earth's land surface is occupied by human activities, and with a continuing expansion of the human population, more land is converted for agriculture, urban development and other human uses (Krausmann *et al.* 2013). With less land available for wild species to inhabit, increasing numbers are threatened by extinction. Habitat degradation and loss are the biggest threat to biodiversity today (Tillman *et al.* 2017). Lost habitats can include, in addition to complete loss, habitat fragmentation - former large areas of habitat are often fragmented into habitat patches separated from each other by fields, towns, roads, or other barriers that limit the free dispersal of species. The unnatural inhospitable environment surrounding fragments often, as a consequence, reduces species dispersal. Many species living in the forest interior are reluctant to move over even a short distance of open land (Rossetti *et al.* 2017). Habitats in fragments can for that reason be lost, and result in local extinction of species.

This paper focuses on bats in Sweden and their dispersal between habitats in the landscape. Bats represent the world's second most species-rich order of mammals and are a significant part of global biodiversity (Wilson & Reeder 2005, Stone *et al.* 2015). Of all bat species, about 75% are insectivorous (Cormier 2014), occupying high trophic levels. Bats react in parallel with a range of taxa to many different stressors, which gives them great potential as bioindicators (Jones *et al*. 2009). With their slow reproduction rates and long lives, they are considered to be bioindicators of biodiversity response to human disturbances (Jones *et al*. 2009, Azam *et al*. 2018). Bats are declining worldwide, a consequence of what is thought to be forest fragmentation. This is supported by the fact that the most threatened species all are adapted to foraging in wooded areas (Safi & Kerth 2004). Many species are dependent on forests for roosting and foraging (Brigham 2007, Kerth & Melber 2009) and most bat species are at some period of their life reliant on forests (Law *et al*. 2016). Bats are highly social animals (Kerth 2008), which means a large number of individuals of local bat colonies can be affected simultaneously by habitat fragmentation. Fragmentation can disrupt commuting routes, resulting in a need to relocate routes in order to reach foraging grounds; forcing longer flights with increased energy needs as a result (Stone *et al.* 2015). Bats have for that purpose been observed to make detours to avoid open areas (Limpens & Kapteyn 1991, Altringham & Kerth 2016) or to find appropriate points to cross (Kerth & Melber 2009, Altringham & Kerth 2016). Some species are more severely affected because they are highly adapted to certain habitats which induces higher commuting costs and restricted dispersal capacity (Safi & Kerth 2004, Azam *et al.* 2018). Relocated routes may have less optimal vegetation cover and could risk exposing them to predators, or wind. If relocating routes are not possible, colonies could be separated from their foraging grounds, possibly forcing them to leave their roost (Stone *et al.* 2015).

By increasing connectivity between fragments, the negative consequences of fragmentation can be mitigated and species movement increased. Connectivity is important for bats' survival (Carlier *et al*. 2019), and it significantly increases species richness and activity (Frey-Ehrenbold *et al.* 2013). Landscape connectivity, defined by Taylor *et al.* (1993) as 'the degree to which the landscape facilitates or impedes movement among resource patches', can be measured by two approaches: structural connectivity and functional connectivity. Structural connectivity refers to the arrangement and relationship between habitat patches in the landscape (With *et al.* 1997, Carlier *et al*. 2019), corridors or stepping-stones are important for dispersal or daily movements (Gelling *et al*. 2007, Frey-Ehrenbold *et al.* 2013). Functional connectivity refers to the probability or capacity of a given species to reach and move in or between patches in the landscape (Taylor *et al.* 1993, Carlier *et al*. 2019).

Lost habitats, or the connectivity between them, especially affect species highly dependent on them. The woodland-specialised species in particular, are reluctant to fly over open landscapes (Ekman & de Jong 1996, Frey-Ehrenbold *et al.* 2013, Altringham & Kerth 2016). Their foraging behaviour, wing morphology and echolocation call are adapted to flying in or close to cluttered vegetation (Neuweiler 1984, Frey-Ehrenbold *et al.* 2013). With short, broad wings, they are manoeuvrable and slow flying, and their echolocation calls are suited for short range detection of prey close to vegetation or water surfaces (Neuweiler 1989). Because they are slow flying, flying over open landscapes could make them particularly vulnerable to predation (Jones & Rydell 1994, Frey-Ehrenbold *et al.* 2013). Why these species avoid open areas is not clear; there are some hypotheses to explain this behaviour of which predator avoidance is one (Limpens & Kapteyn 1991, de Jong 1995, Ekman & de Jong 1996, Verboom 1998). In addition to avoiding open areas, the woodland-specialised species also avoid light because of an intrinsic perception of a higher predation risk, most likely from diurnal birds (Speakman 1991, Rydell *et al.* 1996, Azam *et al*. 2018). Connected landscapes may be of prime importance for these species (Frey-Ehrenbold *et al.* 2013).

Other than limited movement, consequences of habitat fragmentation include those of modern forestry, in which natural forests are clearcutted and new trees that favour timber production are planted. With time the forests regrow, mainly as monocultures (Guldin *et al.* 2007). Many forest adapted species require old, wide and tall trees with cavities or loose, exfoliating bark as day roosts, which becomes a scarce commodity (Barclay & Kurta 2007). Even-aged stands are naturally of the same height, which means most of the tree foliage is in the main canopy. This makes the area within and below the canopy very dense, too dense even for clutter-adapted bats (Guldin *et al.* 2007). Monocultures are unfavourable for bats and other insectivorous animals as it produces prey cycles with less insect species and longer periods between hatch cycles. It eventually results in an ‘explosion’ of these insects, which becomes designated as forest pests. Pesticides in forest settings, loss of old, dead and dying trees, and disturbed nursery and hibernation caves in forests are all causes of population declines (Lacki *et al*. 2007) that can be linked to modern forestry.

As a consequence of natural environments being increasingly fragmented and connecting landscapes threatened from intensified agricultural practises (Verboom 1998, Frey-Ehrenbold *et al.* 2013), forestry (Guldin *et al.* 2007), urbanisation, and expansion of transport infrastructure (Carlier *et al*. 2019, Sher & Primack 2020), the woodland-adapted species are continually deprived of their foraging habitat. They become more vulnerable, and recolonization of abandoned areas even less possible. These species are in fact the ones having suffered most severely from human disturbance in Europe (Safi & Kerth 2004) which has been evident in frequent recordings of population declines in several *Myotis* and *Plecotus* species (Speakman *et al.* 1991, Rydell 1992a).

This study was designed to test the hypothesis that occurrences of species from the genus *Myotis* in urban areas indicate habitat connectivity. By examining if landscape elements with different levels of isolation (isolated ‘islands’, connected ‘islands’, corridors and controls) are utilised, the following questions were intended to be answered:

(1) Are *Myotis* species more frequently observed in habitats with connection to continuous forests, compared to in isolated habitats?

(2) Are patch size, distance to continuous forest, or distance to nearest habitat important factors for occurrence in isolated habitats?

(3) Is habitat selection different in the beginning of summer when nights are light, compared to later in summer when nights are darker?

The most common *Myotis* species in Sweden (de Jong *et al.* 2020), and in Uppsala county (where this study was conducted), are *Myotis brandtii/Myotis mystacinus* and *Myotis daubentonii* (de Jong & Gertz 2001), and these species were also the most common in the study area. In this study, *Myotis brandtii* was not separated from *Myotis mystacinus*. *Myotis brandtii* has been observed to avoid foraging in open areas, preferably hunting in coniferous forests (de Jong 1995, Ekman & de Jong 1996). *Myotis daubentonii* on the other hand usually forage over open water surfaces (Swift & Racey 1983, Rydell *et al.* 1996, Ahlén 2011), but periodically also in forests, on occasions far from open water (Ahlén 2011). Since the *Myotis* species has been found to be dependent on landscape connectivity, I predicted the species to be found in elements with connection to forests (controls, corridors, and connected islands), and not to be found in isolated habitat islands. Because they also have been seen to avoid light, I predict there will be a lower occurrence earlier in the summer compared to later in the summer.

2. Material and methods

2.1 Study area

This study was conducted in collaboration with Tierp municipality. Study sites were consequently located in Tierp, in the east of central Sweden. Data sampling was carried out in July 2021. In order to examine connectivity in urban environments, the sites were chosen mainly in or close to the town of Tierp, each one belonging to one of the four following categories (Figure 1):

[In this context *habitat* is defined as a tree covered area.
50 m was used as an isolation limit based on previous studies by Kelm *et al.* 2014 where *Myotis* species rarely were found more than 50 m from vegetation structures].

Isolated island - isolated habitat 'islands' (more than 50 m from mainland) of forest were used to examine occurrences of forest living bat species (*Myotis* spp), and whether they move over open landscapes to habitat patches.

Corridor - narrow tree corridors between continuous forests were used to examine if connectivity facilitates movement between habitats for the forest-dwelling *Myotis* species.
As it turned out, corridors were scarce and only a few could be found in the study area.

Connected islands - forest 'islands' not completely isolated from the town's surrounding forest, separated only by a small road (two-lane road or gravel road; no more than 20 m from mainland), were used in addition to corridors. The purpose of connected islands was to assess whether they are used by the study species; thus, if they facilitate movement through the landscape.

Control areas - continuous forests surrounding the town of Tierp were used for controls. One forest located on the northeast side, and one on the west side of the town were used for data sampling. Control sites were systematically placed with a minimum distance of 200 metres between locations.

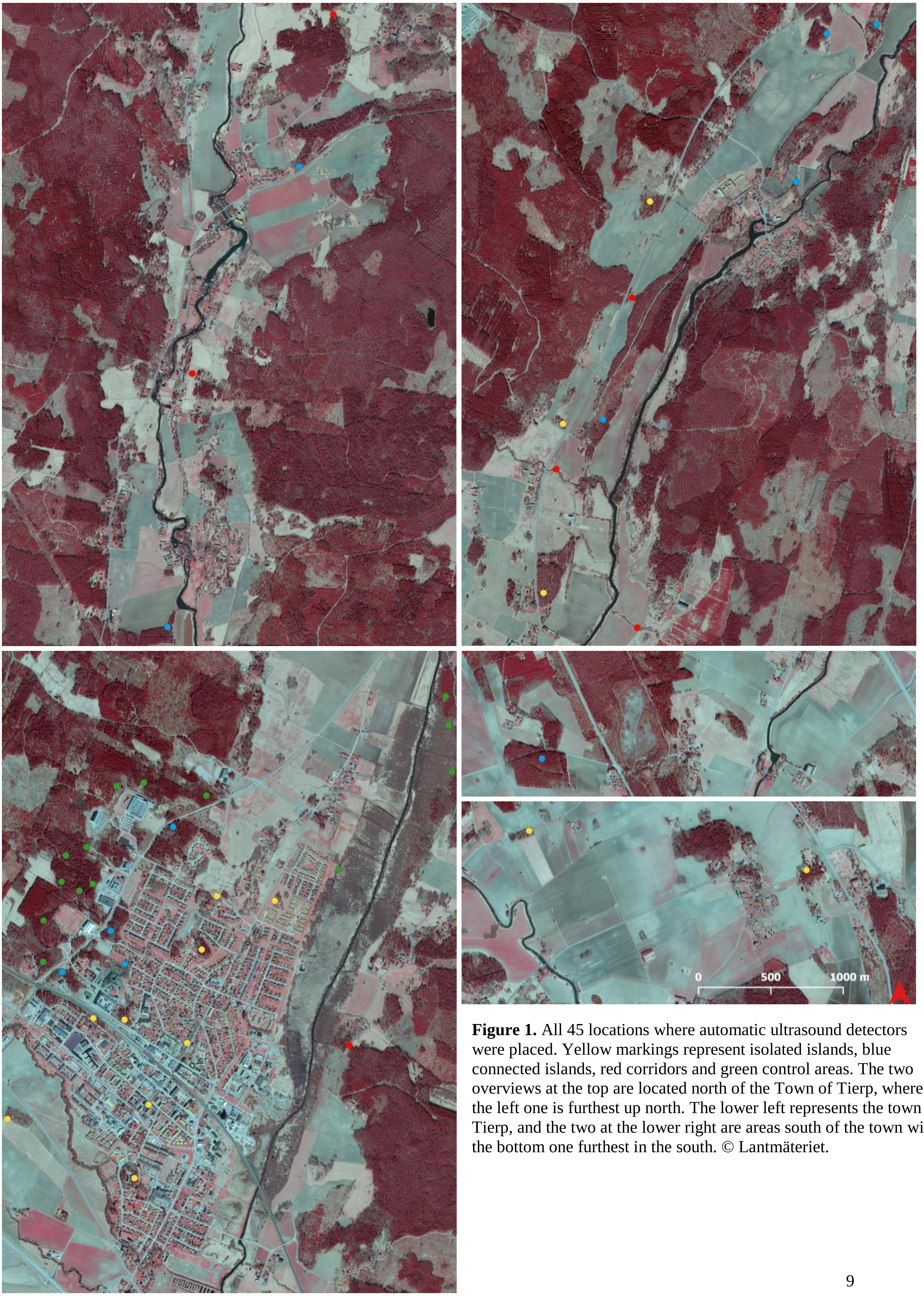

Figure 1. All 45 locations where automatic ultrasound detectors were placed. Yellow markings represent isolated islands, blue connected islands, red corridors and green control areas. The two overviews at the top are located north of the Town of Tierp, where the left one is furthest up north. The lower left represents the town of Tierp, and the two at the lower right are areas south of the town with the bottom one furthest in the south. © Lantmäteriet.

2.2 Sampling

Automatic ultrasound detectors D500X (Pettersson Elektronik AB, Uppsala, Sweden; www.batsound.com) were used to record bat activity at the sites. The detectors were attached to trees approximately two metres above ground, towards the interior of the forest. During 15 nights, three recording attempts were made each night at different locations, making a total of 45 sampling sites. Recordings started around 15 minutes before sundown and stopped about 15 minutes after sunrise. The detectors were placed in sites of the same category (isolated islands/connected islands/corridors/controls) each night and alternated between different categories to the greatest extent possible; the last few nights were mixed because of different numbers of sites for the different categories - 14 isolated islands, 11 connected islands, 6 corridors and 14 controls.

2.3 Data analysis and bat identification

Shape and size of landscape elements, connectivity, and distance between elements were determined by spatial analysis (GIS). Echolocation sound design differs between European bat species, allowing species identification from sound (Frey-Ehrenbold *et al.* 2013). The software program Batsound (Pettersson Elektronik AB) was used for analysis of recorded data. Only *Myotis* recordings were of interest in this study. *Myotis* species were not identified more specifically because echolocation sounds are similar between the species of this genus and difficult to distinguish (Russ & Montgomery 2002, Barataud 2020). Statistical analyses were made in Minitab 19.2020.1 (Minitab, LLC). Alpha level 0,05 was used for all tests. Multiple regression analysis was used to test *Myotis* occurrence on isolated islands as a factor of island size, distance to nearest habitat, distance to forest and date. Nearest habitat could be an isolated or connected island, a smaller habitat patch, or the surrounding forest (Figure 2). The study period was parted into a lighter and darker period, with a breaking point of the 15th of July. The whole study period, and the lighter period (before the 15th), were tested in the regression analysis. Correlation between dates and bat occurrence on isolated islands, connected islands, corridors and controls were also examined.

Figure 2. A potential flyway: adjacent habitats create a possibility for movement. Habitat patches can be used as stepping-stones through the town of Tierp to reach foraging grounds (Tämnarån and surrounding wetland forest). Markings represent study sites; blue are connected islands, yellow isolated islands, and green controls (continuous forest). © Lantmäteriet.

3. Results

The first night of the study was the 6th of July, sundown that night was at 22.09 and sunrise 03.48. The 15th of July (at the breaking point between the light and the dark period) sundown was at 21.57 and sunrise 04.03. The last night of the study was the 24th of July when sundown was at 21.39 and sunrise 04.22. This makes a difference of about an hour in the length of the day between the beginning and end of the study.
The size of isolated islands ranged from 0,5 ha to 10,3 ha. The longest distance to a continuous forest was 1130 metres and the shortest 53 metres. Distance between isolated islands and nearest stepping-stones ranged between 15 and 200 metres. A total of 517 *Myotis* observations were made in all locations; 115 on isolated islands, 23 on connected islands, 88 in corridors and 291 in controls (Table 1 & 2, Appendix).

Table 1. Dates (in July) for bat observations, and number of observations at isolated habitat islands in Tierp, Sweden. Data on area, distance to continuous forest and distance to nearest habitat are given for each island.

Isolated island	Date (July)	Size (ha)	Distance continuous forest (m)	Distance nearest habitat (m)	Observations
I. island 1	19	2,6	486	44	3
I. island 2	19	1	585	82	2
I. island 3	19	1,4	515	80	0
I. island 4	10	2,5	53	30	0
I. island 5	6	2	815	90	0
I. island 6	6	0,5	1130	200	0
I. island 7	6	1	1030	50	0
I. island 8	22	1,6	900	200	28
I. island 9	19	0,75	190	15	2
I. island 10	10	10,3	300	86	2
I. island 11	22	0,9	112	100	63
I. island 12	20	4	170	170	13
I. island 13	10	6,5	55	55	2
I. island 14	10	3,2	170	130	0

Table 2. Dates (in July) for bat observations, and number of observations at connected islands, corridors and controls.

Location	Date (July)	Observations
C. island 1	11	0
C. island 2	20	3
C. island 3	11	2
C. island 4	11	0
C. island 5	11	0
C. island 6	7	0
C. island 7	7	0
C. island 8	22	1
C. island 9	20	16
C. island 10	7	0
C. island 11	7	1
Corridor 1	15	18
Corridor 2	15	2
Corridor 3	15	2
Corridor 4	15	1
Corridor 5	24	55
Corridor 6	24	10
Control 1	8	98
Control 2	23	8
Control 3	12	0
Control 4	8	2
Control 5	8	2
Control 6	8	0
Control 7	12	1
Control 8	23	24
Control 9	24	6
Control 10	24	54
Control 11	12	0
Control 12	12	0
Control 13	23	34

Control 14	23	62

The mean values of *Myotis* observations at the four different categories (Figure 3) points out that the highest numbers of *Myotis* observations were registered in controls, followed by corridors. Isolated islands and connected islands had the least numbers, with the latter having the lowest. A Mann-Whitney u-test had no significance for the mean values of controls in comparison with isolated islands, connected islands or corridors (Table 3). Out of 14 isolated islands, three had high numbers of *Myotis* observations - I. island 8 had 28, I. island 11 had 63, and I. island 12 had 13. Connected islands had only one location (out of 11 in total) with a relatively high number of observations; C. island 9 had 16. All six corridors had observations, of which two had high numbers; corridor 1 had 18, and corridor 5 had 55. Most of the 14 control areas had observations, four had none registered.

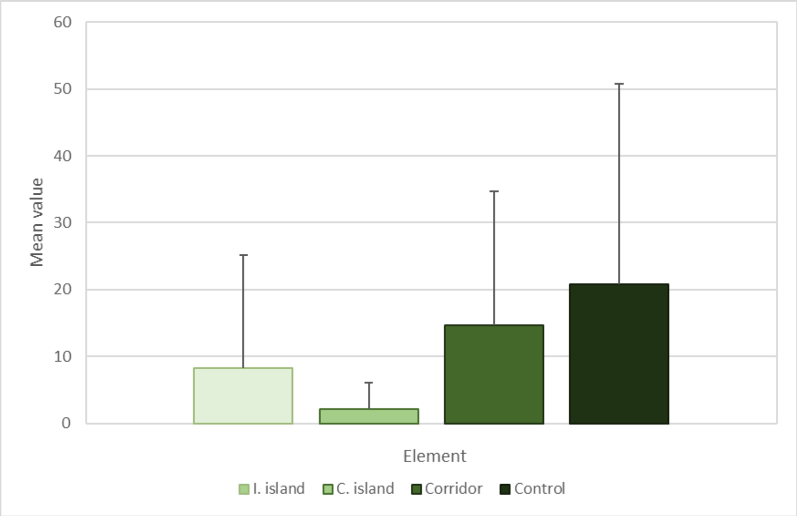

Figure 3. Mean values for *Myotis* observations at isolated islands, connected islands, corridors and controls. Number of locations (n) were 14 for islands and controls, 11 for connected islands and 6 for corridors. Standard deviations (SD) were 17,5 for islands, 4,7 for connected islands, 20,8 for corridors and 30,6 for controls.

Table 3. P-values (Mann-Whitney u-test) represent connection between observations in different elements, or at different time periods in an element (before and after the 15th of July).

Variables	**P-value**
Control - Isolated island	0,301
Control - Connected island	0,067
Control - Corridor	0,741
Isolated island before & after 15th	0,025
Connected island before & after 15th	0,041

Most observations in both isolated and connected islands were made in the darker period, with a significant difference before and after the 15th of July (Mann-Whitney u-test, p < 0,05, Figure 4, Table 3). A Multiple regression analysis showed no significance between *Myotis*' observations on isolated islands and size, distance to nearest habitat or distance to continuous forest. However, there was a positive relation between observations and dates (p < 0,05, Table 4). When islands in the darker period were excluded, there was a positive significance on island size (p < 0,05, Table 5). Controls and dates, corridors and dates, and connected islands and dates had no correlation. Isolated islands and dates were positively correlated (p < 0,05, Table 6).

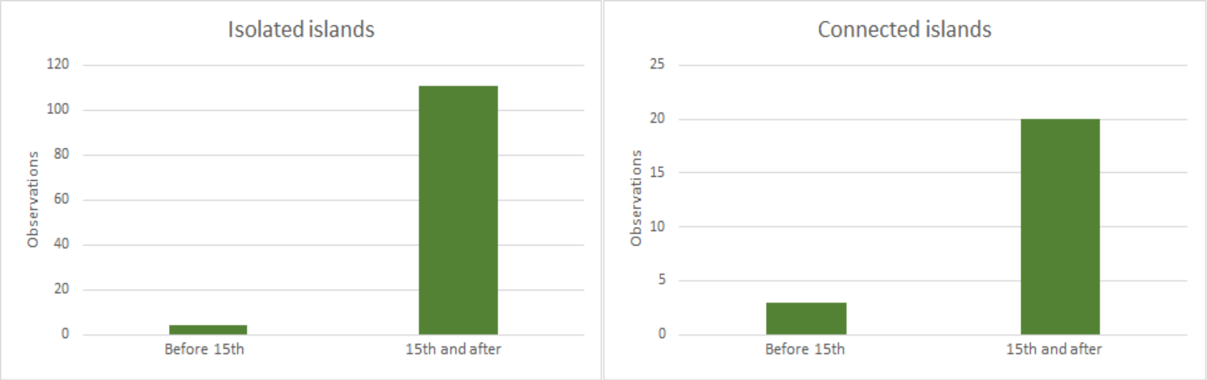

Figure 4. Bat observations before and after the 15th of July at isolated and connected islands.

Table 4. Multiple regression analysis with bat activity as response variable, and size, distance to nearest habitat, distance to continuous forest, and dates for data sampling as predictors on isolated islands for the whole study period.

Variables	P-value
Size	0,521
Distance to nearest habitat	0,337
Distance to continuous forest	0,541
Date	0,037

Table 5. Multiple regression analysis with bat activity as response variable, and size, distance to nearest habitat, distance to continuous forest, and dates for data sampling as predictors on isolated islands before the 15th of July.

Variables	P-value
Size	0,004
Distance to nearest habitat	0,591
Distance to continuous forest	0,276
Date	0,203

Table 6. R-values represent correlation coefficients (Pearson) between *Myotis* observations and dates at isolated islands, connected islands, corridors and controls. P-values for each one.

Value	I. island	C. Island	Corridors	Controls
R-value	0,561	0,555	0,663	0,229
P-value	0,037	0,077	0,151	0,432

4. Discussion

This study confirms that the forest living *Myotis* species need connected habitats for foraging. The importance of connected habitats for bat dispersal has been described in several previous studies (Boughey *et al*. 2011, Hale *et al.* 2012, Frey-Ehrenbold *et al.* 2013), however, this pattern was only obvious during the light summer period. The highest activity of *Myotis* was evident in mainland habitats (controls), and the activity decreased with increased isolation. Isolated islands had, however, higher activity than connected islands. This was unexpected, but one reason for this may be limited data; during the darker period, half of the isolated islands were visited, whilst only three out of the 11 connected islands were. Another explanation might be that all connected islands were separated from continuous forest by a small road (two-lane road or gravel road), which possibly could have been considered a barrier to bats. A study has in fact shown bats to avoid areas in proximity to roads - even to small, two-lane roads (Altringham & Kerth 2016, but see also Kerth & Melber 2009). If so, it means that the important factor was not the distance, but the light.

A positive relation was found between dates and observations in isolated islands. In both isolated and connected islands, most observations were made in the latter half of July. In Sweden summer nights are light around the solstice of summer at which time bat foraging takes place around midnight, when bats have minimum light intensity exposure (Rydell 1992b). Later in summer nights are darker, which could explain the dispersal to more isolated habitats later in July. The result from this study agrees with previous studies which have registered a shift in habitat use in response to light condition changes. *Myotis mystacinus* has, for example, been observed to hunt in more open areas later in the summer, as the nights become darker (Nyholm 1965, Ekman & de Jong 1996). This avoidance behaviour during the lighter period provides good support for the predator hypothesis, that the forest living species avoid crossing open ground in light conditions in order not to be spotted by diurnal predators. The fact that they do not cross open ground earlier in the summer is of concern in terms of conservation, because it is at that time colony formation takes place. A fragmented landscape will prevent colony formation in the area and be an impoverished landscape. Connected landscapes are thereby crucial for reproduction and survival of these species in the area.

During the light period, in the end of June and beginning of July, female bats are pregnant which reduces manoeuvrability and increases susceptibility to predation (Speakman 1991). Pregnant females form maternity colonies that could involve hundreds of individuals. When time for parturition, pups are left in the day roosts while females forage, to return again at night to nurse. Lactating females may for that reason be limited in the distance they can travel at night to forage, and the criteria for roost selection may be different than before birthing (Chruszcz & Barclay 2002, Barclay & Kurta 2007). Being less restricted, males and nonreproductive females can travel greater distances and often use other roosts during spring and summer, roosting either solitarily or in small groups (Barclay & Kurta 2007). This study, taking place during the month of July, was carried out in time of parturition. However, there was no registration of gender or lactating females, so we cannot know if any lactating bats were observed in isolated islands. There is a possibility that lactating females considered the distance to cross too far from the roost and thus avoided flying to more isolated habitats.

In addition to fragmentation, decreased bat occurrence in urban environments may also be exacerbated by streetlights at night (Azam *et al.* 2018, Laforge *et al.* 2019) since it is avoided by many forest adapted species (Rydell 1992, Altringham & Kerth 2016, Azam *et al.* 2018). Lights affect a significant part of surrounding habitat, and could spill onto, and fragment, flyways or commuting routes (Stone *et al.* 2015, Azam *et al.* 2018, Laforge *et al.* 2019). In Sweden, *Myotis* species have been observed only with a distance from streetlights (Rydell 1992a, Stone *et al.* 2015). In central Tierp, isolated islands were surrounded by illuminated streets, which potentially could have had some influence on dispersal patterns. This is supported by the fact that the most central island (isolated island 3) was the only island with no *Myotis* activity during the darker period, even though it was not the most isolated, or the smallest island. In order to reach it, bats would have had to cross several open areas illuminated by streetlights. Since this study was not designed to test streetlight induced fragmentation, no conclusions can however be drawn from this.

Other factors likely to affect bat occurrences are insect availability and weather conditions. At nights of low prey availability bats have been found less frequent in their usual foraging sites, presumably to search for alternative sites. In times of low insect availability or low temperatures, bats can enter torpor to save energy (Hickey & Fenton 1996); naturally, spending less time in flight.

No correlation was found between bat activity and dates for control areas, corridors and connected islands. Activity and dates were positively correlated for isolated islands, suggesting bat numbers were somewhat the same in the less isolated areas throughout the study period, and dispersed to more isolated habitat later in July when nights became darker. There was a positive connection between island size and bat observations for the lighter period. Previous studies by Ahlén (1983) and Ekman & de Jong (1996) support this result, where it was demonstrated island size, and isolation, are important factors for occurrence. Choosing islands of larger size could minimise time spent in the open for species that avoid open areas (Ekman & de Jong 1996). Oprea *et al.* 2009 demonstrated, in agreement with previous studies, that overall species richness and abundance decreases with urbanisation. They found the highest bat diversity in urban areas to be concentrated in urban parks. Gili *et al.* 2020 found an increase in occurrence of forest living species, particularly of *Myotis* species, with an increase in the area of discontinuous woodland in an urban area. All of which highlights the importance of larger habitat areas to maximise the prospects of maintained biodiversity in highly modified environments.

In this study, the most important factor determining bat occurrence appeared to be the light conditions. Isolated habitat with a distance of 15 to 200 metres from another habitat (which was the distance range between isolated islands and its nearest habitat in this study), seems to be a barrier for *Myotis* species in light conditions, but not in dark conditions. Light seems thereby to enhance the isolation effect and be a bigger impediment for habitat use than fragmentation alone. For that reason, habitat islands are isolated during the early, light nights of Swedish summer, but connected and used as stepping-stones when nights become darker later in summer. Previous studies by Frey-Ehrenbold *et al.* 2013 compared linear and patchy elements to assess shape effects and connectivity. As it turned out, shape is of much less importance than the area overlayed by vegetation, and whether the arrangement of elements is sufficient to allow access. Linear and patchy elements are equally valued as foraging habitats and stepping-stones. They also found higher levels of connectivity the closer an isolated habitat was to a continuous forest, and in agreement with what has previously been mentioned, the importance of size of landscape elements.

The results from this study support the hypothesis that occurrence of forest living bats indicate habitat connectivity in urban environments; *Myotis* species are more frequently observed in elements with connection to forests (continuous forests and corridors) than in habitat islands (connected and isolated). Without connected habitats, forest living bat species avoid habitat patches in light conditions, and dispersal is thereby limited in the early summer. During light nights, patch size is an important factor for bat occurrence, while distance to forest, or nearest habitat is not. Because of this effect of the light conditions on bat dispersal, connected habitats are highly important in areas under this influence, in order to facilitate movement through the landscape. Further studies could assess at what level of illuminance the forest living bats begin to disperse to more isolated habitats. Possible differences in dispersal patterns between habitat islands in areas illuminated at night and areas not illuminated at night could also be examined.

4.1 Conclusion

The importance of connectivity for bats was highlighted in this study where the highest occurrences of *Myotis* was observed in continuous forest and corridors. Light exposure enhances the isolation effect of fragmentation, thus islands within 15 - 200 metres from another habitat are isolated during the light nights of Swedish summer, but connected and used as stepping-stones in the darker nights later in the summer. Larger islands were used more frequently than small islands by the forest living bats, thereby minimising time spent flying in open landscapes. Linear and patchy elements increase connectivity and provide valuable corridors and stepping-stones to bats highly dependent on connected landscapes for dispersal.

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References

Ahlén I. (1983). The bat fauna of some isolated islands of Scandinavia. Oikos 41: 352-358.

Ahlén, I. (2011). Fladdermusfaunan i Sverige. Arternas utbredning och status. Kunskapsläget 2011. [The Bat fauna of Sweden. Knowledge on distribution and status 2011]. Fauna & Flora 106: 2–19.

Altringham J., Kerth G. (2016). Bats and Roads. In: Voigt C., Kingston T. (eds) Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer, Cham. https://doi.org/10.1007/978-3-319-25220-9_3

Azam C., Le Viol I., Bas Y., Zissis G., Vernet A., Julien JF., Kerbiriou C. (2018).
Evidence for distance and illuminance thresholds in the effects of artificial
lighting on bat activity. Landscape and Urban Planning 175: 123–135.

Barclay RMR., Kurta A. (2007). Ecology and behaviour of bats roosting in tree cavities and under bark. In: Lacki J., Hayes JP., Kurta A. (eds) Bats in forests: Conservation and management. The Johns Hopkins University Press, Baltimore.

Barataud M. (2020). Acoustic Ecology of European Bats - Species Identification, Study of their Habitats and Foraging Behaviour. 2nd edition. p. 209-211. Biotope éditions & French National Museum of Natural History, Paris.

Boughey KL., Lake IR., Haysom KA., Dolman PM. (2011). Effects of landscape-scale broadleaved woodland configuration and extent on roost location for six bat species across the UK. Biological Conservation 144: 2300–2310.

Hickey BC., Fenton MB. (1996). Behavioural and thermoregulatory responses of female hoary bats, Lasiurus cinereus (Chiroptera: Vespetilionidae), to variations in prey availability. Ecoscience 3, 414–422.

Brigham MR. (2007). Bats in forests: what we know and what we need to learn. In: Lacki J., Hayes JP., Kurta A. (eds) Bats in forests: Conservation and management. The Johns Hopkins University Press, Baltimore.

Callahan EV., Drobney RD., Clawson RL. (1997). Selection of summer roosting sites by Indiana bats (Myotis sodalis) in Missouri. Journal of Mammalogy 78: 818–825.

Carlier J., James Moran J., Aughney T., Roche N. (2019). Effects of greenway development on functional connectivity for bats. Global Ecology and Conservation 18: e00613.

Chruszcz BJ., Barclay RMR. (2002). Thermoregulatory ecology of a solitary bat, *Myotis evotis,* roosting in rock crevices. Functional ecology 16: 18-26.

Cormier A. (2014). Species diversity and activity of insectivorous bats in three habitats in La Virgen de Sarapiquí, Costa Rica. Revista de biología tropical 62: 939-46.

de Jong J. (1995). Habitat use and species richness of bats in a patchy landscape. Acta Theriologica 3.

de Jong J., Gertz J. (2001). Inventering av fladdermöss 2000. [Inventory of bats 2000]. Rapport Nr 04. Länsstyrelsen i Stockholms län, Stockholm. http://www.diva-portal.org/smash/get/diva2:851914/FULLTEXT01.pdf. Date visited: 2021-09-17.

de Jong J., Gylje Blank S., Ebenhard T., Ahlén I. (2020). Fladdermusfaunan i Sverige – arternas utbredning och status 2020. [The Bat fauna of Sweden. Knowledge on distribution and status 2020]. Fauna & flora 115: 2–16.

Ekman M., de Jong J. (1996). Local patterns of distribution and resource utilization of four bat species (Myotis brandtii, Eptesicus nilssoni, Plecotus auritus and Pipistrellus pipistrellus) in patchy and continuous environments. Journal of Zoology 238: 571-580.

Frey-Ehrenbold A., Bontadina F., Arlettaz R., Obrist MK. (2013). Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. Journal of Applied Ecology 50: 252–261.

Gelling M., Macdonald DW., Mathews F. (2007). Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. Landscape Ecology 22: 1019–1032.

Gili F., Newson SE., Gillings S., Chamberlain DE., Border JA. (2020). Bats in urbanising landscapes: habitat selection and recommendations for a sustainable future. Biological Conservation 241: 108343.

Guldin JM., Emmingham WH., Carter SA, Saugey DA. (2007). Silvicultural practices and management of habitat for bats. In: Lacki J., Hayes JP., Kurta A. (eds) Bats in forests: Conservation and management. The Johns Hopkins University Press, Baltimore.

Hale JD., Fairbrass AJ., Matthews TJ., Sadler JP. (2012). Habitat Composition and Connectivity Predicts Bat Presence and Activity at Foraging Sites in a Large UK Conurbation. PLOS ONE 7: e33300.

Jones G., Rydell J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions: Biological Sciences 346: 445–455.

Jones G., Jacobs DS, Kunz TH., Willig MR., Racey PA. (2009). Carpe noctem: the importance of bats as bioindicators. Endangered Species Research 8: 93–115.

Kelm DH., Lenski J., Kelm V., Toelch U., Dziock F. (2014). Seasonal bat activity in relation to distance to hedgerows in an agricultural landscape in central Europe and implications for wind energy development. Acta Chiropterologica 16: 65–73.

Kerth G. (2008). Causes and consequences of sociality in bats. Bioscience 58: 737–755.

Kerth G., Melber M. (2009). Species-specific barrier effects of a motorway on the habitat use of two threatened forest-living bat species. Biological conservation 142: 270-279.

Krausmann F., Erb KH., Gingrich S., Haberl H., Bondeau A., Gaube V., Lauk C., Plutzar C., Searchinger, TD. (2013). Global human appropriation of net primary production doubled in the 20th century. Proceedings of the National Academy of Sciences 110: 10324-10329.

Lacki MJ., Hayes JP., Kurta A. (2007). Bats in Forests: Conservation and Management. The Hopkins University Press, Baltimore

Laforge A, Pauwels J., Faure B., Bas Y., Kerbirio, C., Fonderflick J., Besnard A. (2019). Reducing light pollution improves connectivity for bats in urban landscapes. Landscape Ecology 34: 793–80.

Law B., Park KJ., Lacki MJ. (2016) Insectivorous Bats and Silviculture: Balancing Timber Production and Bat Conservation. In: Voigt C., Kingston T. (eds) Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer, Cham. https://doi.org/10.1007/978-3-319-25220-9_5

Limpens HJGA., Kapteyn K. (1991). Bats, their behaviour and linear landscape elements. Myotis 29: 39-48.

Neuweiler G. (1984). Foraging, echolocation and audition in bats. Naturwissenschaften, 71: 446–455.

Neuweiler G. (1989). Foraging ecology and audition in echolocating bats. Trends in Ecology and Evolution 4: 160-166.

Nyholm ES. (1965). Zur Ökologie von Myotis mystacinus (Leisl.) und M. daubentoni (Leisl.) (Chiroptera). Annales Zoologici Fennici 2: 77-123.

Oprea M., Mendes P., Vieira TB., Ditchfield AD. (2009). Do wooded streets provide connectivity for bats in an urban landscape? Biodiversity Conservation 18: 2361–2371.

Rossetti MR., Tscharntke T., Aguliar R., Batáry R. (2017). Responses of insect herbivores and herbivory to habitat fragmentation: A hierarchical meta-analysis. Ecology Letters 20: 264-272.

Russ JM., Montgomery WI. (2002). Habitat associations of bats in Northern Ireland: implications for conservation. Biological Conservation 108: 49–58.

Rydell J. (1992a). Exploitation of Insects around Streetlamps by Bats in Sweden. Functional Ecology 6: 744-750.

Rydell J. (1992b). Occurrence of bats in northernmost Sweden (650N) and their feeding ecology in summer. Journal of Zoology 227: 517-529.

Rydell J., Entwistle A., Racey PA. (1996). Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk. Oikos 76: 243-252.

Safi K., Kerth G. (2004). A comparative analysis of specialization and extinction risk in temperate-zone bats. Conservation Biology 18: 1293–1303.

Sher AA., Primack RB. (2020). An introduction to conservation biology. 2nd edition. Oxford University Press, New York.

Speakman JR. (1991). Why do Insectivorous Bats in Britain Not Fly in Daylight More Frequently? Functional Ecology 5: 518–524.

Speakman JR., Racey PA., Catto CMC., Webb PI., Swift SM., Burnett AM. (1991) Minimum summer populations and densities of bats in N.E. Scotland, near the northern borders of their distributions. Journal of Zoology 225: 327-345.

Stone EL., Harris S., Jones G. (2015). Impacts of artificial lighting on bats: a review of challenges and solutions. Mammalian Biology 80: 213–219.

Swift SM., Racey PA. (1983). Resource partitioning in two species of vespertilionid bats occupying the same roost. Journal of Zoology 200: 249-259.

Taylor PD., Fahrig L., Henein K., Merriam G. (1993). Connectivity is a vital element of landscape structure. Oikos 68: 571e572.

Tillman D., Clark M., Williams DR., Kimmel K., Polasky S., Packer C. (2017). Future threats to biodiversity and pathways to their prevention. Nature 546: 73–81.

Verboom B. (1998). The use of edge habitats by commuting and foraging bats. IBN scientific contribution 10. DLO Institute for forestry and nature research (IBN-DLO), Wageningen.

Wilson DE., Reeder DM. (2005). Mammal Species of the World: A Taxonomic and Geographic Reference, third ed. Johns Hopkins University Press, Baltimore, USA**.**

With KA., Gardner RH., Turner MG. (1997). Landscape Connectivity and Population Distributions in Heterogeneous Environments. Oikos 78: 151-169.

Appendix

Table A1. Coordinates for all study locations (isolated islands, connected islands, corridors, and controls), dates in July when automatic ultrasound detectors recorded bat activity, and number of *Myotis* observations at each site.

Location	X coordinate	Y coordinate	Date	Observations
I. island 1	639193	6693650	19	3
I. island 2	639088	6693281	19	2
I. island 3	638556	6692797	19	0
I. island 4	638341	6692807	10	0
I. island 5	638624	6691703	6	0
I. island 6	638722	6692210	6	0
I. island 7	638987	6692637	6	0
I. island 8	637749	6692111	22	28
I. island 9	639592	6693618	19	2
I. island 10	640756	6696426	10	2
I. island 11	635055	6678326	22	63
I. island 12	636971	6678054	20	13
I. island 13	640891	6697598	10	2
I. island 14	641493	6699139	10	0
C. island 1	644577	6704956	11	0
C. island 2	638128	6693125	20	3
C. island 3	638460	6693410	11	2
C. island 4	638891	6694128	11	0
C. island 5	641168	6697628	11	0
C. island 6	642506	6699276	7	0
C. island 7	643062	6700366	7	0
C. island 8	636390	6689364	22	1
C. island 9	638557	6693181	20	16
C. island 10	642718	6700301	7	0
C. island 11	643665	6701768	7	1
Corridor 1	640107	6692619	15	18
Corridor 2	641369	6698472	15	2
Corridor 3	643837	6703524	15	2

Corridor 4	644814	6706011	15	1
Corridor 5	640844	6697284	24	55
Corridor 6	641405	6696185	24	10
Control 1	638244	6693687	8	98
Control 2	637995	6693196	23	8
Control 3	639120	6694344	12	0
Control 4	637997	6693482	8	2
Control 5	638337	6693734	8	2
Control 6	638295	6693989	8	0
Control 7	638501	6694411	12	1
Control 8	638690	6694434	23	24
Control 9	638121	6693749	24	6
Control 10	638152	6693931	24	54
Control 11	640030	6693837	12	0
Control 12	640769	6695030	12	0
Control 13	640790	6694832	23	34
Control 14	640813	6694506	23	62

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