
Occurrence of Moths in Boreal Forest Corridors

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Abstract: We studied the utility of riparian corridors in boreal forest landscapes as habitats and dispersal routes for forest-associated noctuid and geometrid moths in northern Finland. We collected moths with baited traps to investigate their occurrence and abundance in four habitat types—forest interior, forest edge, forested corridors, and clearcuts—along riparian zones. This was done with a sampling design in which the four habitat types were nested within four riparian systems. Corridors were strips of forest 30–70 m wide surrounded by clearcuts and sapling stands. Trap sites in forest interior were more than 100 m away from the nearest forest edge within large (>50 ha) patches of mature (timber volume > 100 m³/ha), spruce-dominated forests. Forest-edge trap sites were in the same forest patches within 25 m from the nearest clearcut edge, and clearcut trap sites were in recent (<10-year-old) clearcuts >50 m away from the nearest mature forest. A total of 6485 specimens, representing 57 moth species, were captured during the 6-week trapping period in late June–August 1999. The number of species and total number of individuals did not differ among the forested habitats (interior, edge, corridor) but were significantly lower in clearcuts. A consistent pattern across the nine species we examined in more detail was the low number of individuals captured in clearcuts. In general their abundance in corridors was equal to that observed in forest interiors and edges. Two species tended to occur in corridors in higher numbers than in forest-interior habitats. Our results suggest that corridors in boreal forest landscapes serve as breeding habitats or dispersal routes for the moths and may direct the movements of these forest-associated species. Results from studies showing positive effects of corridors on dispersal or population persistence should not, however, be used to justify more habitat destruction.

Presencia de Mariposas Nocturnas en Corredores de Bosques Boreales

Resumen: Estudiamos la utilidad de los corredores riparios en paisajes forestales boreales como hábitats y rutas de dispersión de mariposas noctuidas y geométridas asociadas a bosques en el norte de Finlandia. Recogimos mariposas nocturnas con trampas cebadas para investigar su presencia y abundancia en cuatro tipos de hábitat (interior de bosque, borde de bosque, corredores arbolados y zonas taladas) a lo largo de zonas riparias. Esto se hizo con un diseño de muestreo en el que los cuatro tipos de hábitat se anidaron en cuatro sistemas riparios. Los corredores eran franjas de bosque de 30–70 m de ancho rodeados de zonas taladas y conjuntos de árboles jóvenes. Las trampas en el interior del bosque estaban a más de 100 m del borde más cercano en fragmentos grandes (<50 ha) de bosques maduros (volumen de madera >100 m³/ha) dominados por abetos. Los sitios de borde de bosque estaban en los mismos fragmentos a 25 m del borde más cercano y las trampas en zonas taladas estaban en sitios recientemente deforestados (<10 años) >50 m del bosque maduro más cercano. Recogimos un total de 6485 especímenes de 57 especies durante el período de 6 semanas de trampeo a fines de junio-agosto de 1999. No hubo diferencia alguna en el número de especies y el total de individuos entre los hábitats boscosos (interior, borde y corredor), pero estos valores fueron significativamente menores en las zonas taladas. En las zonas taladas hubo un menor número de individuos capturados en las nueve especies examinadas con más detalle. En general, su abundancia en los corredores fue igual a la observada en el interior y en el borde del bosque. Dos especies tendieron a ocurrir en mayor número en los corredores que en los hábitats del interior del bosque. Nuestros resultados sugieren que los corredores en paisajes de bosques boreales sirven como hábitat reproductivo o como rutas de dispersión para mariposas nocturnas y pueden dirigir los movimientos de estas especies asociadas a bosques. Los resultados de estudios que muestran los efectos positivos de los corredores sobre la dispersión o persistencia de poblaciones no deben, sin embargo, ser utilizados para justificar mayores pérdidas de hábitat.

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Introduction

Boreal forest landscapes have been subjected to considerable changes during the past decades because of commercial forestry (Bryant et al. 1997; Esseen et al. 1997). Consequently, forest management is the most important threat for a number of species in boreal Fennoscandia (Anonymous 1986; Berg et al. 1994). To reconcile the conflict between forestry and biodiversity maintenance, a more conservation-oriented forest-management planning system was implemented in the Nordic countries during the 1990s (Rülcker et al. 1994; Halman et al. 1996; Angelstam & Petterson 1997). In this system, hereafter referred to as landscape ecological forest management, entire landscapes, usually of some tens of thousands of hectares, are considered one management unit. The goal is to maintain viable populations of all naturally occurring species in the area and to enhance their movement between different patches of forests, while at the same time harvesting timber in an economically sustainable way. One of the tools in landscape-level planning for biodiversity is to design corridors and other structures for the dispersal of individuals in managed landscapes (Mönkkönen 1999).

Both theoretical (e.g., Anderson & Danielson 1997; Hanski 1999) and empirical (e.g., Dunning et al. 1995; Machtans et al. 1996; Schmiegelow et al. 1997) studies have shown that landscape connectivity enhances population viability. Habitat corridors are frequently used to provide connectivity, but surprisingly little is known about their role as habitat and dispersal routes (Niemelä 2001). Beier and Noss (1998) reviewed the evidence for corridors enhancing or diminishing population viability and individual dispersal and found only 32 studies focusing specifically on this relationship, with less than half of these providing persuasive data for inferences. These studies provided support for positive effects and no evidence for negative effects of corridors (cf. Hobbs 1992; Simberloff et al. 1992; Rich et al. 1994).

Most studies reviewed by Beier and Noss (1998) dealt with vertebrates, and the lack of knowledge seems to be particularly pronounced concerning insects and other invertebrates. Little information exists on how corridors may serve as habitats or dispersal routes for boreal taxa other than birds and mammals (e.g., Machtans et al. 1996; Gustafsson & Hansson 1997; Schmiegelow et al. 1997; Darveau et al. 1998). Most insect studies, both in the boreal settings and elsewhere, have been carried out on carabid ground beetles (Burel 1989; Charrier et al. 1997; Petit & Usher 1998; Fournier & Loreau 1999) and butterflies (Sutcliffe & Thomas 1996; Haddad 1999; Haddad & Baum 1999). Studies on butterflies have so far focused on population viability and individual dispersal among species associated with open habitats such as meadows (Sutcliffe & Thomas 1996; Schultz 1998; Haddad 1999, 2000; Haddad & Baum 1999), whereas there

have been no studies on corridor use by butterflies or moths associated with forest habitats.

To study the usefulness of corridors in boreal forest landscapes as habitats and dispersal routes for boreal forest moths, we carried out an observational study in northern Finland. Observational studies on animal movements and occurrence in corridors may provide important information in real landscapes, although they cannot unequivocally test for the positive effect of corridors on population persistence (Nicholls & Margules 1991; Inglis & Underwood 1992). Beier and Noss (1998) particularly called for attempts to detect extracorridor movements to further test for corridor usefulness in fragmentation-sensitive species.

We used baited traps to collect moths inhabiting mature boreal forests and investigate their occurrence and abundance in four habitat types along riparian zones: forest interior, forest edge, forested corridors, and clearcuts. If moths actively avoided corridors, their numbers would be lower there than in forest interiors, and one could conclude that corridors are of little importance to moths as habitat or dispersal routes. If the abundance of moths is higher in corridors than elsewhere, corridors likely function as movement routes. It is not necessary, however, to observe such "packing" to infer dispersal through corridors, because the presence alone or breeding of moths in the corridor demonstrates them to be of use. Connectivity across generations may be the most important aspect of dispersal in habitat corridors for insects and other small animals dispersing relatively short distances. If no differences between habitats (including clearcut areas) are found, then moths are not strictly confined to old-growth forests. Corridors may still have value as breeding habitats but evidently little value for dispersal. We designed our study to determine the occurrence and abundance of moths in corridors compared with other habitats created by the landscape ecological management planning system in Fennoscandia (Angelstam & Petterson 1997; Mönkkönen 1999).

Study Area and Methods

The study areas were in Pudasjärvi, northern Finland (lat. 65°30'N, long. 28°00'E), in the northern boreal zone (Kalliola 1973). The landscape is mainly forested (approximately 70% of the total land area) and characterized by a large proportion of peat land (29%; pine bogs, open fens). Due to intensive forestry, the proportions of sapling stands (28% of total land area) and young forests (29%) are high. Most of sapling stands and young forests are planted in pine (*Pinus sylvestris*) trees. Only about 15% of the land area is comprised of mature forests (total timber volume >100 m³/ha), of which 6.5% are pine-dominated and 8.5% spruce-dominated (*Picea abies*) (Reunanen et al. 2002). Because of the long history of

forest use, all mature forests in the area have been selectively harvested at least once during the nineteenth and early twentieth centuries, and they do not represent true old-growth conditions. In spruce-dominated mesic forests, the shrub layer is usually sparse and the field layer is dominated by bilberry (*Vaccinium myrtillus*), with *Vaccinium uliginosum*, *Deschampsia flexuosa*, and *Lycopodium* spp. in moist sites and *Calluna vulgaris*, *Empetrum nigrum*, and *Vaccinium vitis-idaea* in dryish and mesic sites. Typical of spruce forests is a thick and species-rich cover of moss, including *Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp., and *Polytrichum* spp.

According to the planning instructions, corridors should be established along creeks, rivers, or other aquatic habitats and their widths should vary between 30 and 70 m (Halman et al. 1996). Corridors are created in a step-wise fashion. Beginning with a block of mature forest, first the other side of the planned corridor is harvested, creating an edge. The opposite side of the corridor is harvested after the first harvested side has reached a canopy height of one-third of the original. We placed traps in four different habitats along each of four creeks: (1) forest interiors (>110 m from the nearest edge) within mature (timber volume >100 m³/ha) spruce forest to represent initial conditions where both sides of the creek are unharvested; (2) forest edges (17–25 m away from the edge in mature spruce forest) to represent the phase of corridor design in which one side of the waterway is clearcut and the other side is still intact; (3) corridors (on average 50 m wide; range 30–70 m) surrounded by recent clearcuts and sapling stands (tree height 4–6 m), with strips of mature spruce forest along creeks and traps placed approximately in the middle of the corridors; (4) clearcuts (at least 50 m away from the nearest mature forest), to represent control for detecting extra-corridor occurrence with forest on both sides of the creek harvested and no or few trees retained.

We had four replicates assigned into four blocks (riparian systems). A block contained one trap site of each habitat type along the same creek (Fig. 1). We placed three traps at each trap site, for a total of 48 traps. To standardize environmental conditions, the traps were located <5 m from the nearest creek of 1–3 m in width and about 1.5 m above ground level. Traps were attached to lower branches of large spruce trees. The distance between the three traps within a trap site was 25 m.

Fieldwork was carried out between 28 June and 10 August 1999, which covered almost the entire flight season of *Xestia* moths. We used sugar-bait traps developed by M. Soininmäki and P. Välimäki. The trap was a 20-L plastic bucket with a lid, with three circular entrance holes 7 cm in diameter on the upper part of the bucket. The entrances continue into the bucket via plastic tubes 5 cm long, which made escape from the trap difficult. The bait was in the middle of the bucket with 2 dL of

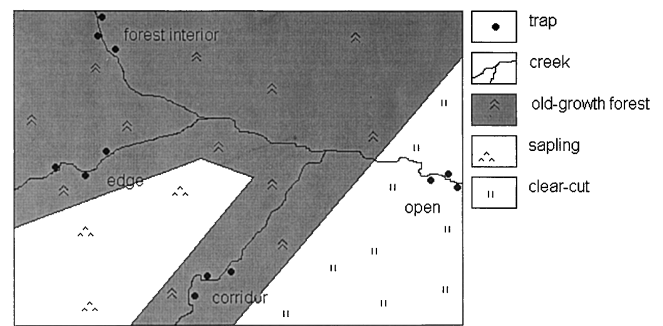


Figure 1. Schematic presentation of the design of trap sites within one block of the four habitat types.

bait liquid soaked into foam plastic. Under the bait was a plastic funnel, which led to a lower chamber with chloroform-poisoned air. Chloroform was in a 2-dL bottle with a small hole for evaporation.

The bait consisted of light beer (10 L), sugar (4 kg), honey (200 g), and yeast (50 g). The mixture was fermented at 20° C for about 1 week before use. The traps were checked every 9 days (four times during the study period). Each time, the containers of bait liquid and chloroform were refilled and all moths were packed in plastic boxes and taken to a freezer for later identification. All individuals in the samples were sexed.

Within a 10-m radius around each trap, we measured the circumference and average height of all tree individuals. These values were transformed to basal area per hectare. We surveyed the composition of the field-layer vegetation using 20 sampling plots of 0.25 m² around each trap. Plots were situated 1 m from one another along two 10-m transects extending at opposite directions from traps. The cover of dominant plant species (>10% of total cover) in each plot was recorded.

Spruce was the dominant tree species in all forested habitats, but birch (*Betula* spp.) comprised a significant proportion of total basal area. In clearcuts the dominant tree species was birch. Bilberry was the dominant species of plant cover in the field layer in all habitats except clearcuts, although it was also common in clearcuts (Table 1).

We used the 16 trap sites (sum of the three traps) as independent statistical units in the analyses. We used mixed analysis of variance (ANOVA) models (type III sum of squares) to analyze the data. For species richness and total abundance we fitted models in which block was entered as a random factor and habitat (interior, edge, corridor, and clearcut) as a fixed factor. For individual species, in addition to block and habitat main effects, models included sex as a fixed factor and the interaction term habitat × sex. A significant interaction between habitat and sex is expected if there are differences among habitat types in suitability for reproduction and dispersal, and if dispersal is biased toward either sex. If the main effect of habitat was significant, we used a least-significant-difference (LSD) post-hoc test to study

Table 1. Average total basal area, tree species composition, and bilberry cover for the different habitat types examined in this study.^a

	Interior	Edge	Corridor	Clearcut
Basal area				
total (dm ² /ha) ^b	69.0 (53.1–93.6)	72.0 (63.5–80.5)	87.6 (62.9–114.0)	0.17 (0–0.68)
spruce (%) ^c	77 (59–98)	78 (65–93)	80 (67–88)	0
birch (%) ^c	20 (2–36)	13 (7–26)	13 (9–20)	48 (0–48)
other trees ^d (%) ^c	3 (0–6)	9 (0–16)	7 (3–13)	52 (0–52)
Bilberry cover (%)	59 (40–77)	73 (47–85)	60 (42–80)	18 (5–45)

^aMinimum and maximum values are given in parentheses.

^bTotal basal area is the average basal area summed over tree species.

^cPercentage of the total basal area.

^d*Pinus sylvestris*, *Populus tremula*, *Alnus incana*, and *Salix caprea*.

differences between habitats in more detail. We used correlation analysis to examine the relationship between the abundance of moths and the composition of tree species or coverage of bilberry across trap sites.

Results

We collected 6485 moth specimens representing 57 species in three different families, thyatirids (Thyatiridae), geometrids (Geometridae), and noctuids (Noctuidae). For most species we caught only one or a few specimens. No species trapped during fieldwork is considered threatened. The most abundant species, *Xestia speciosa*, accounted for 50%, and the 9 most abundant species (Table 2) accounted for 92% of all individuals.

We included in the analyses the moth species for which more than 100 individuals were collected. For less common species, the power of statistical tests is low. All these nine species are associated with coniferous forests, particularly *Xestia* moths, which are considered old-forest specialists and monophagous species, with their larvae feeding mainly on bilberry (Table 2). *Xestia* moths have a 2-year life cycle, and in our study

area adult moths occur mainly in odd years (Mikkola & Jalas 1976). Other species included in this study are considered less specialized in their habitat and food requirements and may occur in many types of forested habitat, feeding on a number of plants (Table 2). However, the habitat associations and food plant preferences of these species are not yet fully known.

Species richness and total moth abundance (sum across the nine species) were lower in clearcuts than in other habitats (Table 3). No differences in species richness and total abundance were found between forest interior, forest edges, and corridors (Fig 2).

There were significant differences among habitat types in the abundance of *X. speciosa* (Table 3). The species was less abundant in clearcuts but occurred with equal abundance in the three forested habitats (Fig. 2). Males were captured more often than females (2024 vs. 1236 individuals) but were captured consistently across habitat types (i.e., habitat–sex interaction was not significant) (Table 3). The same pattern—lower abundance in clearcuts and equal abundance in all three forested habitats—was found for *Eurois occultus*, *Chloroclysta truncata*, and *C. citrata*. For *C. citrata* more than three times more males than females (146 vs. 46) were captured.

Table 2. Habitat preferences, food plants, and sample sizes for the moth species, of which more than 100 individuals were captured.

Species	Family	Habitat preference ^a	Main food plants	No. individuals
<i>Xestia speciosa</i>	Noctuidae	old, moist, spruce-dominated forests	<i>Vaccinium myrtillus</i> , <i>V. uliginosum</i>	3260
<i>Xestia rhaetica</i>	Noctuidae	old, moist, spruce-dominated forests with thick moss layer	<i>Vaccinium myrtillus</i> , <i>V. uliginosum</i>	590
<i>Eurois occultus</i>	Noctuidae	various kinds of forests, edges, gardens	<i>Vaccinium myrtillus</i> ^b	359
<i>Diarsia mendica</i>	Noctuidae	moist, open forests and shrublands	<i>Vaccinium myrtillus</i> ^b	307
<i>Chloroclysta citrata</i>	Geometridae	open forests, forest edges, bogs	<i>Vaccinium myrtillus</i> ^b	189
<i>Chloroclysta truncata</i>	Geometridae	open forests, forest edges, bogs	<i>Vaccinium myrtillus</i> ^b	181
<i>Eulitbis populata</i>	Geometridae	coniferous forests	<i>Vaccinium myrtillus</i>	392
<i>Entepbria caesiata</i>	Geometridae	spruce forests	<i>Vaccinium myrtillus</i> ^b	532
<i>Arichanna melanaria</i>	Geometridae	spruce mires and pine bogs	<i>Ledum palustre</i>	179

^aPreference based on Mikkola and Jalas (1976, 1985), Mikkola et al. (1989), and Skou (1991).

^bFood preferences are not well known.

Table 3. Analysis of variance for species richness, total abundance, and abundance of the nine most common moth species.

Source of variation	df	MS	F	p
Species richness				
habitat	3	11.73	14.95	0.001
block	3	0.90	1.14	0.384
error	9	0.79		
Total abundance				
habitat	3	218533.2	13.08	0.001
block	3	61806.2	3.70	0.055
error	9	16707.7		
<i>Xestia speciosa</i>				
habitat	3	36540.3	24.69	<0.001
sex	1	19404.5	13.11	0.002
habitat × sex	3	4210.3	2.85	0.062
block	3	7838.1	5.30	0.007
error	21	1479.9		
<i>Xestia rbaetica</i>				
habitat	3	1457.9	5.14	0.008
sex	1	283.8	1.24	0.279
habitat × sex	3	107.7	0.38	0.769
block	3	670.0	2.36	0.100
error	21	283.8		
<i>Eurois occultus</i>				
habitat	3	272.6	6.80	0.002
sex	1	148.8	3.71	0.068
habitat × sex	3	39.9	0.99	0.415
block	3	83.8	2.09	0.132
error	21	40.09		
<i>Diarsia mendica</i>				
habitat	3	140.9	1.22	0.328
sex	1	520.0	4.49	0.046
habitat × sex	3	26.0	0.23	0.878
block	3	487.1	4.21	0.018
error	21	115.8		
<i>Eulitbis populata</i>				
habitat	3	600.8	2.71	0.070
sex	1	2080.1	9.41	0.006
habitat × sex	3	292.5	1.32	0.293
block	3	574.6	2.60	0.079
error	21	221.1		
<i>Entepbria caesiata</i>				
habitat	3	1833.1	7.70	0.001
sex	1	5724.5	23.75	<0.001
habitat × sex	3	1631.1	6.77	0.002
block	3	512.8	2.13	0.127
error	21	241.1		
<i>Arichanna melanaria</i>				
habitat	3	198.3	4.02	0.021
sex	1	30.0	0.61	0.444
habitat × sex	3	5.865	0.12	0.948
block	3	240.8	4.89	0.010
error	21	49.28		
<i>Cboloroclysta truncata</i>				
habitat	3	106.8	7.93	0.001
sex	1	42.8	3.18	0.089
habitat × sex	3	10.6	0.79	0.514
block	3	68.5	5.09	0.008
error	21	13.5		
<i>Cboloroclysta citrata</i>				
habitat	3	134.4	5.15	0.008
sex	1	294.0	11.3	0.003
habitat × sex	3	45.8	1.76	0.187
block	3	98.8	3.79	0.026
error	21	26.1		

There were significant differences among habitat types in the abundance of *X. rbaetica* (Table 3). Although the species seemed to occur in lower abundance in clearcuts, the difference between corridors and clearcuts was not significant (Fig. 2). A similar pattern was found for *Eulitbis populata* (Table 3; Fig. 2).

Entepbria caesiata was the only species with significant habitat-by-sex interaction, indicating that the sexes differed in their abundance patterns among habitats (Table 3; Fig. 2). Many fewer females than males were captured (52 vs. 480 individuals). Females were more common in forest interiors and edges than in clearcuts, but no differences were found between corridors and other habitats. Males were more common in corridors than any other habitat. A similar pattern was found for *Arichanna melanaria*. Both males and females of this species were observed in much higher numbers in corridors than in forest interior and clearcuts (Fig. 2).

No significant habitat-related differences were found in *Diarsia mendica* (Table 3), even though this species showed a lower abundance in clearcuts (30 individuals) than in forest interiors, edges, or corridors (104, 75, 94 individuals, respectively). Also in this species more males than females were captured (218 vs. 89).

There was no correlation across trapping sites between the basal area of trees and the abundance of any moth species. Additionally, bilberry cover was not correlated with the abundance of moths.

Discussion

Most moth species occurred in relatively high numbers in corridors, indicating that corridors may serve as habitat or dispersal routes for forest-associated species. An increase in the amount of edge habitat did not have a strong negative effect on moth densities in our study area because none of the species showed lower abundance at edges or in corridors. A more or less consistent pattern across the species was the low abundance in clearcuts. Moreover, two species were observed in higher numbers in forest corridors than in forest interiors. Such packing may result from dispersal along corridors. Because the movements of moths were not directly studied, it is impossible to say on the basis of our study whether boreal-forest corridors direct the flight of moths, as shown by Haddad (1999) for butterflies associated with open habitats.

It is widely accepted that landscape connectivity is species-specific, and even closely related species may differ in their ability to use corridors depending on their behavioral adaptations (Gustafsson & Hansson 1997; Mönkkönen & Reunanen 1999). Mönkkönen (1999) suggests that the species most likely benefiting from corridors in the landscape are those that have moderate dispersal abilities and intermediate habitat requirements. Spe-

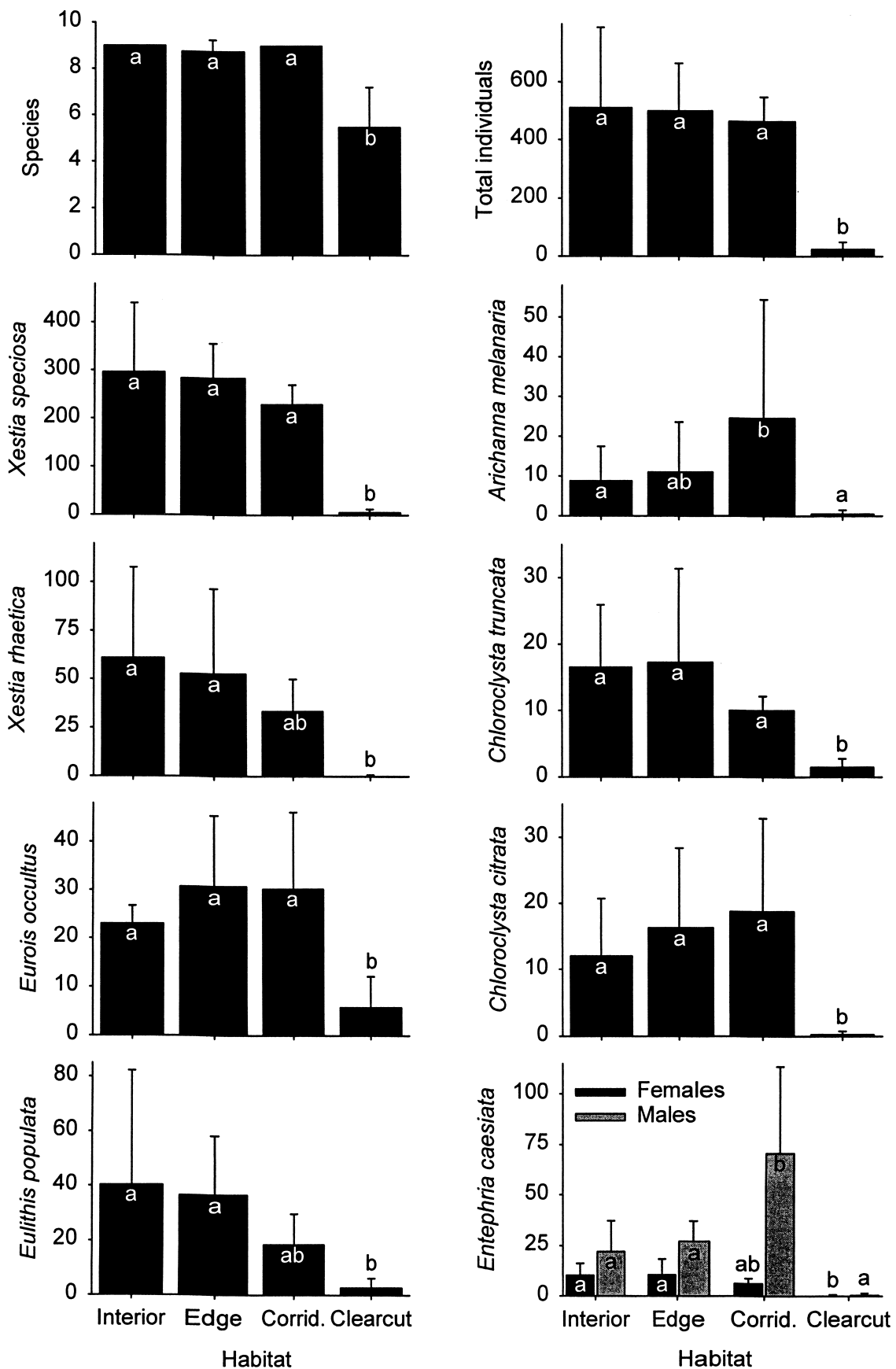


Figure 2. Number of moth species, total number of individuals, and number of individuals for most abundant moth species captured in the four habitat types (corrid., corridor). Each bar denotes average value over the four blocks. Error bars are 1 SD. Lettering above bars refers to the results of least-significant-difference post-hoc tests. Bars with the same letter do not differ from one another. For *Entephria caesiata*, results are depicted separately for females and males because analysis of variance showed a significant interaction between habitat and sex (Table 3).

cies that are not restricted to any one habitat type (habitat generalists) are capable of using many habitat types in their movement between habitat patches and for reproduction. For such species, the role of habitat corridors is small at best. On the other end of the continuum are species that are habitat specialists and poor dispersers. They cannot use corridors for dispersal or reproduction because conditions in narrow strips of habitat surrounded by a totally unfamiliar habitat type are so different from habitat interiors, or because they simply cannot travel long distances between suitable habitats (Mönkkönen 1999). The moth species we studied are likely the kind of species that benefit from corridors. Our results showed that they are forest specialists but do not seem to avoid edges. Moreover, their low abundance in clearcuts may indicate that their dispersal abilities are limited across unfor-ested habitats, but direct observations are needed to confirm this.

Our study did not differentiate between dispersing and reproducing individuals, and we cannot make conclusions about the utility of boreal-forest corridors as habitat versus dispersal routes for moths. Our results suggest, however, that the moths occurred in lower numbers in clearcuts and were able to use corridors. The net effect of forest corridors on the population persistence of boreal species depends on how corridors are related to habitat loss. If corridors result in an increase in the total amount of old-forest habitat (reduced habitat loss), this would have a positive effect on the population sizes of most, if not all, forest-associated species. In this case, however, a conflict may emerge between ecological and economic goals. To the contrary, if corridors are used to justify more total harvesting of forests, leading to habitat loss, the net effect will likely be negative. Many authors have argued that landscape configuration has a much smaller effect on population persistence than habitat availability (e.g., McGarigal & McComb 1995; Fahrig 1997; Trzcinski et al. 1999; but see Villard et al. 1999). In real-world situations the question is often whether limited conservation funds would be better spent on corridors or augmenting existing conservation areas—in other words, whether there is a tradeoff between assigning the given forest area to corridors versus forest reserves (Niemelä 2001). Our results show that moth abundance was as high in elongated, riparian-strip corridors as in forest interiors and no tradeoff necessarily exists, but further studies are needed to distinguish between the hypothesis that corridors facilitate movements and the hypothesis that corridors provide habitat for these moths.

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