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Title	Altitudinal Change of Habitat Preference in Ants of Swiss Jura
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Citation	Low temperature science. Ser. B, Biological sciences, 37, 59-66
Issue Date	1980-03-15
Doc URL	<a href="https://hdl.handle.net/2115/17848">https://hdl.handle.net/2115/17848</a>
Type	departmental bulletin paper
File Information	37_p59-66.pdf



## Altitudinal Change of Habitat Preference in Ants of Swiss Jura<sup>1</sup>

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*Abstract* Altitudinal change of habitat preference in some ant species studied in Swiss Jura is reported. At lower altitudes they more prefer forest or its margin, but at higher altitudes the preference for grassland habitats increases. This affected the similarities among habitats and the interspecific relationships through the nest sites. As the reason of the habitat change, their need for enough sunshine to maintain their colonies under cold climate was more likely than the interspecific competitions.

### Introduction

Any field census of ants is actually undertaken along two environmental gradients, horizontal and altitudinal. Along the horizontal gradient we find various patterns of their habitat preferences (4, 6, 10, 19, etc.). On the other hand, along the altitudinal gradient we can see different ant communities at different altitude according to the gradual change of climatic conditions, especially the temperature.

Although there are many studies made with respect to one of the two aspects mentioned, few studies were carried out with the intention of separating the effects of two gradients. Consequently, it is often difficult to know whether the habitat preference of each species is so rigid that it does not change altitudinally. The purpose of the present study is to analyze the distribution of ants by intentionally recording changes along the two gradients mentioned.

### Census Area and Methods

Swiss Jura is a mountain chain occupying the western part of Switzerland. Its highest point is of about 1,500 m, i. e. slightly lower than the average timberline in Switzerland (1,800 m). Consequently the area is covered with various trees from the foot to the top. The dominant trees are *Quercus* and *Carpinus* below 600 m, *Corex* and *Fagus* at 600 to 800 m, *Fagus* and *Sylvaticus* at 800 to 1,100 m, *Abies* and *Fagus* at 1,100 to 1,300 m, and *Acer* and *Fagus* near the top. The census was carried out in July, 1978, at three altitudes: Coinsins and the vicinity (400 to 500 m), Arzier

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<sup>1</sup> Received for publication October 25, 1979. Contribution No. 2196 from the Inst. Low Temp. Sci. (This research was supported by Grant-in-Aid for Encouragement of Young Scientist from the Ministry of Education.)

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and the vicinity (900 to 1,000 m), Chalet à Roch (1,400 to 1,500 m). The climates of these districts differ from one another. According to the records of Weather Agency of Switzerland from 1901 to 1960, the mean temperature during the ant active season (April to October) is ca. 15°C at Coinsins, ca. 12°C at Arzier and ca. 8°C near the top. The precipitation during the same period is ca. 650 mm, 900 mm and 1,100 mm respectively. Thus, temperature and precipitation differ 3 to 4°C and 200 to 250 mm per 500 m.

At each altitude four habitats, bareland, grassland, forest margin and forest, were chosen. In each habitat nests were searched five times each for 30 minutes, in total 150 minutes. When a nest was found some individuals were collected in a glass tube for the identification and the nest site was recorded with the following symbols: Ba, bare spots with no grass cover; St, under stones; Le, under leaf litter; Gr, roots of grasses; Ms, under mosses; Du, under dead trees; Di, in dead trees; Tw, in dead twigs; Md, with a big mound; Cr, in the crack of rocks.

The distribution was analyzed by the following indices.

Diversity ( $D$ ) and Prosperity ( $P$ ) of each habitat:

$$D = \frac{1}{\sum_i (n_i/N)^2} \quad (17)$$

$$P = N \cdot D \quad (\text{A reformed Morisita's index, 15})$$

where  $n_i$  and  $N$  are respectively the nest abundances of species  $i$  and of all species.

Similarity ( $S$ ) between two habitats:

$$S = \frac{2 \sum_i n_{1i} n_{2i}}{(D_1 + D_2) N_1 N_2} \quad (\text{A reformation of Morisita's } C_s, 11)$$

where  $n_{ij}$ ,  $N_i$  and  $D_i$  are the nest abundance of species  $i$ , the total nest abundance and the diversity in habitat 1 respectively,  $n_{2i}$ ,  $N_2$  and  $D_2$  are those in habitat 2.

Distributional breadth ( $\beta$ ) of each species, calculated by the following procedures (2):

$$M_j(X) = \frac{X_j(\log X_j - \log Z) - \sum_i N_{ij} \log(N_{ij}/Y_i)}{\sum_j X_j \log X_j - Z \log Z}, \quad d_j = \frac{M_j(X)}{\sum_{i \rightarrow j} M_j(X)}$$

$$P_{ij} = \frac{N_{ij}}{\sum_j d_j k \cdot N_{ij}}, \quad \beta = \left[ \frac{1}{\sum_j (d_j k P_{ij}^2)} - 1 \right] \left[ \frac{1}{k-1} \right]$$

where  $X_j$ , the total nest abundance in habitat  $j$ ;  $Y_i$ , the total nest abundance of species  $i$ ;  $Z$ ,  $\sum_j X_j$  or  $\sum_i Y_i$ ;  $N_{ij}$ , nest abundance of species  $i$  in habitat  $j$ ;  $d_j k$ , weighting factor. In the present study 10,000 was applied for  $k$ .

Resemblance of nesting sites ( $\gamma_{ih}$ ) between two species  $i$  and  $h$ :

$$\gamma_{ih} = 1 - \frac{1}{2} \sum_j d_j k |P_{ij} - P_{hj}| \quad (2)$$

$P_{ij}$  and  $P_{hj}$  are calculated with the same procedures as in  $\beta$ , applying the following factors:  $X_j$ , the total nest abundance in a nest site  $j$ ;  $N_{ij}$ , nest abundance of species  $i$  in  $j$ ; the others are the same as in  $\beta$ .

**Results**

In total 439 nests of 32 species were discovered (Table 1). At low altitude (henceforth L), 196 nests of 23 species were found: 17 nests/5 species in bareland (LB), 69/17 in grassland (LG), 83/15 in forest margin (LM), 27/2 in forest (LF). Out of the four habitats, LG ( $D=7.4$ ,  $P=512$ ) and LM (7.2, 595) were diverse and prosperous, but LB (2.8, 48) and LF (1.9, 52) rather simple and poor (Fig. 1). At middle altitude (M), 143 nests of 23 species were found: 19/8 in bareland (MB), 70/20 in grassland (MG), 43/10

**Table 1.** Number of nests discovered. B, G, M and F are bareland, grassland, forest margin and forest respectively. L, M and H mean low, middle and high altitude. T, total

Species	Altitude & Habitat														
	400-500 m					900-1,000 m					1,400-1,500 m				
	LB	LG	LM	LF	T	MB	MG	MM	MF	T	HB	HG	HM	HF	T
<i>Formica</i>															
<i>fuscus</i>	0	7	9	0	16	2	7	4	0	13	0	2	0	0	2
<i>rufibarbis</i>	2	3	1	0	6	0	1	0	0	1	0	0	0	0	0
<i>cunicularia</i>	0	1	3	0	4	0	2	0	0	2	0	0	0	0	0
<i>lemanii</i>	0	0	0	0	0	0	0	0	0	0	0	4	5	0	9
<i>sanguinea</i>	0	1	0	0	1	0	1	1	0	2	0	0	0	0	0
<i>bruni</i>	0	4	0	0	4	0	0	0	0	0	0	0	0	0	0
<i>exsecta</i>	0	0	0	0	0	0	3	0	0	3	0	0	0	0	0
<i>polystena</i>	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
<i>rufa</i>	0	0	1	0	1	1	0	0	0	1	0	0	0	0	0
<i>pratensis</i>	0	3	0	0	3	0	1	0	0	1	0	0	0	0	0
<i>lugubris</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	5	5
<i>Polyergus</i>															
<i>rufescens</i>	0	1	2	0	3	0	0	0	0	0	0	0	0	0	0
<i>Lasius</i>															
<i>niger</i>	9	14	18	0	41	7	8	4	0	19	0	0	0	0	0
<i>alienus</i>	1	5	19	0	25	0	4	0	0	4	0	0	0	0	0
<i>flavus</i>	0	6	10	0	16	1	8	1	0	10	0	1	0	0	1
<i>Myrmica</i>															
<i>ruginodis</i>	1	0	6	16	23	2	5	20	10	37	0	8	6	0	14
<i>scabrinodis</i>	0	1	5	0	6	0	5	1	0	6	0	9	0	0	9
<i>laevinodis</i>	0	1	2	0	3	0	1	1	0	2	0	0	0	0	0
<i>sabuleti</i>	0	1	0	0	1	1	1	1	0	3	0	1	1	0	2
<i>lobicornis</i>	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1

Species	Altitude & Habitat														
	400-500 m					900-1,000 m					1,400-1,500 m				
	LB	LG	LM	LF	T	MB	MG	MM	MF	T	HB	HG	HM	HF	T
<i>sulcinodis</i>	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
<i>schenki</i>	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
<i>Leptothorax</i>															
<i>nylanderi</i>	0	0	0	11	11	0	0	0	0	0	0	0	0	0	0
<i>acervorum</i>	0	0	0	0	0	1	1	0	1	3	0	0	0	0	0
<i>muscorum</i>	0	0	0	0	0	0	1	0	0	1	0	4	0	0	4
<i>nigriceps</i>	0	0	0	0	0	0	0	0	0	0	0	6	0	0	6
<i>gredleri</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Camponotus</i>															
<i>ligniperda</i>	0	0	2	0	2	0	2	0	0	2	0	0	0	0	0
<i>Tetramorium</i>															
<i>caespitum</i>	4	17	3	0	24	4	11	0	0	15	2	9	0	0	11
<i>Tapinoma</i>															
<i>erraticum</i>	0	1	1	0	2	0	3	0	0	3	0	0	0	0	0
<i>Diplorhoptrum</i>															
<i>fugax</i>	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0
<i>Manica</i>															
<i>rubida</i>	0	0	0	0	0	0	0	9	0	9	0	31	4	0	35
T	17	69	83	27	196	19	70	43	11	143	2	77	16	5	100

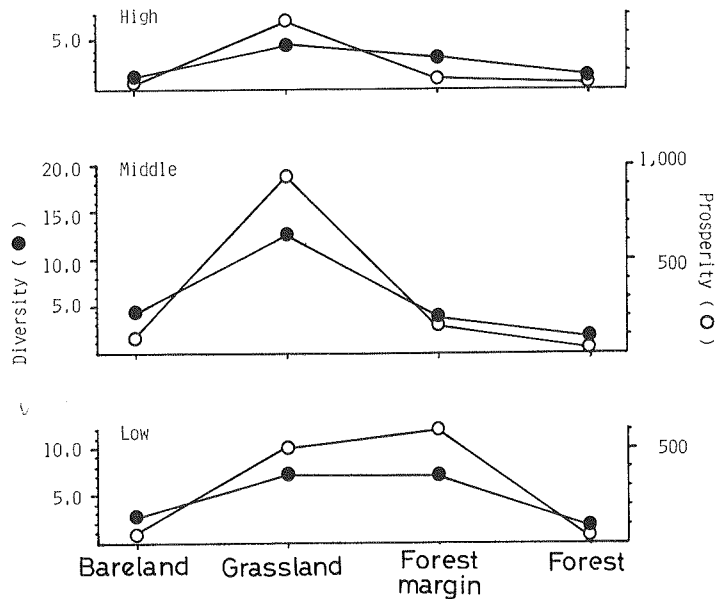


Fig. 1. Diversities and prosperities of 12 habitats

in forest margin (MM), 11/2 in forest (MF). MG was extremely diverse (12.9) and prosperous (940) while MF was very simple (1.2) and poor (13). MB (4.7, 89) and MM (3.6, 153) were relatively simple and poor. Thus, most species concentrated in MG (Fig. 1). At high altitude (H), 100 nests of 13 species were discovered: 2/1 in bareland (HB), 77/12 in grassland (HG), 16/4 in forest margin (HM), 5/1 in forest (HF). HG was relatively diverse and prosperous compared with other habitats:  $D=4.7$ ,  $P=361$  in HG, 3.3 and 53 in HM, 1.0 and 2 in HB, 1.0 and 5 in HF (Fig. 1). Calculating the total diversity and prosperity at each altitude with  $N$ = the total nest abundance in each altitude and  $n_i$ = the nest abundance of a species  $i$  in the altitude,  $D$  decreased gradually from  $L$  (9.2) to  $M$  (8.4) but steeply from  $M$  to  $H$  (5.6) while  $P$  linearly decreased from  $L$  to  $H$  (1,796 at  $L$ , 1,203 at  $M$ , 558 at  $H$ ).

Similarity among 12 habitats is depicted in Fig. 2. Setting the similarity limit at  $S=0.5$ , the habitats are divided into five groups: I. LB-LG-LM-MB-MG; II. LF-MM-MF-HM; III. HB; IV. HG; V. HF. In the group I, *Formica rufibarbis*, *F. fusca*, *F. cunicularia*, *Lasius niger*, *L. alienus*, *L. flavus* and *Tetramorium caespitum* were commonly dominant. On the other hand, in the habitats of group II, all being simple and poor, only *Myrmica ruginodis* was commonly dominant. HB and HF were nearly defaunated, consequently, different from other habitats. HG possessed some highland-typical species such as *Leptothorax nigriceps*, *Le. muscorum*, *F. lemani*, etc., and was different from other habitats.

In Fig. 3 some dominant species with five or more nests found at each altitude are clustered by the index  $\gamma$ . Setting the overlapping limit at  $\gamma=0.5$ , they are divided into four groups at  $L$ : I. *T. caespitum*—*F. rufibarbis*—

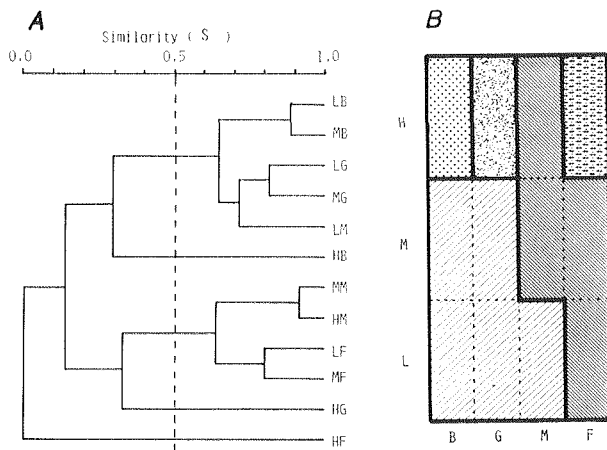


Fig. 2. Similarities among 12 habitats. A. Dendrogram clustering the habitats with the average-linkage method (3). B. Clustering of habitats, setting the similarity limit at  $S=0.5$ . Symbols are the same as in Table 1.

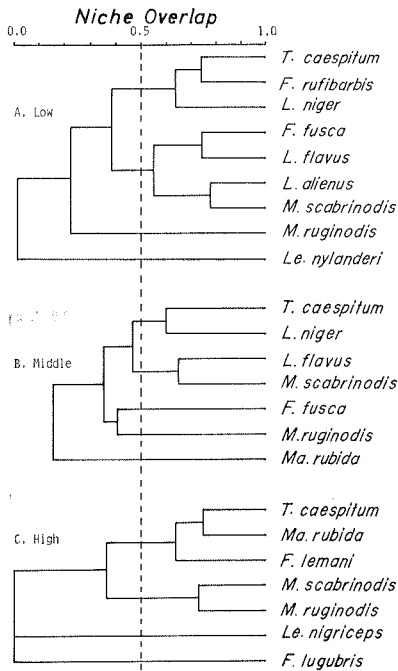


Fig. 3. Dendrograms clustering dominant species in accordance with  $\gamma$ , using average-linkage method

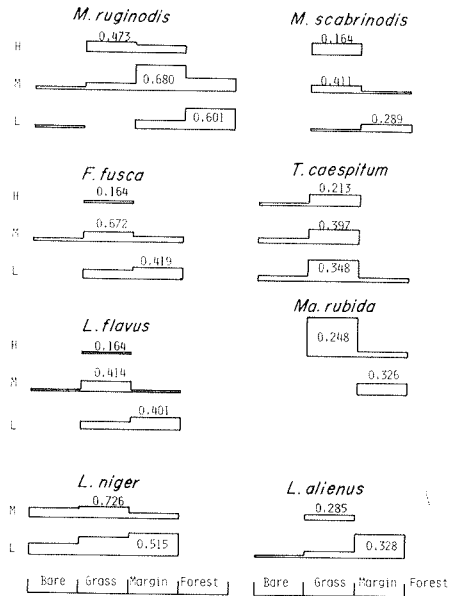


Fig. 4. Distribution of some dominant species. Numerals, distributional breadth ( $\beta$ ). Symbols, cf. Table 1. In many species the distribution center slides to grassland at higher altitude.

*L. niger*, nesting at St, Gr and Ba (the symbols, cf. section for methods); II. *F. fusca*—*L. flavus*—*L. alienus*—*M. scabrinodis*, at St, Gr and Le; III. *M. ruginodis*, at Le, Du and Di; IV. *Le. nylanderii*, at Tw. At M they were grouped into five: I. *T. caespitum*—*L. niger*, at Ba and Gr; II. *L. flavus*—*M. scabrinodis*, at St and Gr; III. *F. fusca*, at St, Ba, Le and Ms; IV. *M. ruginodis*, at Gr, Le, Du and Di; V. *Ma. rubida*, at Gr and Le. At H four groups: I. *T. caespitum*—*Ma. rubida*—*F. lemami*, at St and Gr; II. *M. scabrinodis*—*M. ruginodis*, at Gr; III. *Le. nigriceps*, at Cr; IV. *F. lugubris*, making Md. One of the important findings is the altitudinal change of species pairing. For instance, at M *T. caespitum* nested at Ba and Gr and *Ma. rubida* inhabited Le ( $\gamma=0$ ). At H, however, the both species occupied St and Gr ( $\gamma=0.774$ ). Such difference of  $\gamma$  was also seen between *F. fusca* and *L. flavus* ( $\gamma=0.745$  at L but 0.253 at M) and between *M. scabrinodis* and *M. ruginodis* (0.314 at L, 0.346 at M but 0.728 at H).

As shown above, the habitat LM was more similar to MG than to MM, and MF was more similar to HM than to HF. Furthermore,  $\gamma$  between two given species sometimes varied very conspicuously by altitude. One of the causes of these phenomena should be the altitudinal change of habitat preference in some species (Fig. 4). For instance, *M. ruginodis* more pre-

ferred the forest at L, the forest margin at M but the grassland and the forest margin at H. *F. fusca*, *L. niger*, *L. flavus*, *L. alienus*, *M. scabrinodis* and *Ma. rubida* more preferred the forest margin at lower altitude but the grassland at higher altitude. Only *T. caespitum*, a grassland dweller at L, did not change the preference. *Le. nylanderi* found only in Tw at L was never discovered at higher altitudes. Thus, the species which change the habitats according to altitude have at least two common characteristics: 1. At lower altitude they more prefer forest or its margin than grassland. 2. They are rather generalists than specialists as to nest site preference. Near the top of the mountain, their distribution breadthes ( $\beta$ ) are smaller than at lower altitudes (Fig. 4).

### Discussion

The present study shows that the habitat preference of ants is changeable with altitude. As the factors causing the habitat change the followings are conceivable: I. Biotic factors such as predators, interspecific competitions for food, nest materials or nest sites, and elimination by extremely dominant species. II. Abiotic factors such as temperature, insolation and precipitation. If the biotic factors are main reasons these habitat-changeable species must be affected seriously by predators, competitors or eliminators in the lower altitude grassland and/or in the higher altitude forest. But in the low altitude grassland no species who seemingly drive out other species can be detected. In the forest near the top of Jura *F. lugubris* forms a big supercolony (5) which should be avoided by other ants (10). But this should not be a main reason of the habitat change, because even out of this supercolony no nest of any species was found in forests. On the other hand, the altitudinal difference of climate seems to be more serious to the ants: Most species of ants are omnivorous. Furthermore, the habitat changeable species are flexible in nest site and habitat preferences. Owing to these characteristics it should not be difficult for them to change nest sites and even habitats under different climates. Thus, under warmer climate they should more prefer forest margins or even forests, but under cooler climate opener habitats. Obviously such plasticity should have limits particular to the species. Furthermore, the cold climate seems to be critical for ants to maintain their colonies by producing enough callows every year. For instance, the mean life span of adult workers in *Formica yessensis* (8) and *F. japonica* (9) was estimated at about one year. Considering other reports on the longevity of labo-cultured workers (1, 16), the mean life span of adult workers may be nearly one year or less in many species, too. Then, to keep its average size, a colony must produce annually at least as many new workers as those present at the beginning of the active season. For this purpose, the colony needs sufficient amount of heat during the breeding season, and the change of habitat preference is probably one of such strategies.

### Acknowledgments

I wish to express my sincere gratitude to Prof. Shôichi F. Sakagami for his reading through the manuscript. Cordial thanks are also due to Dr. Heinrich Kutter and Mr. Daniel Cherix for their helps in identification of ant species.

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