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Circadian and year-round activity of the land snails *Candidula unifasciata* and *Helicella itala* in grasslands of the Swiss Jura mountains (Gastropoda: Stylommatophora: Helicidae)

With 6 Figures and 1 Table

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Abstract. The circadian and year-round activity patterns of the land snails *Candidula unifasciata* and *Helicella itala* were examined in dry, calcareous grasslands of the Swiss Jura mountains. *Helicella itala* showed a bimodal distribution of daily activity with one peak around midnight and another after dawn, whereas *C. unifasciata* was most active around midnight. In both species, the circadian activity was negatively correlated with air temperature. The two species differed in their seasonal activity patterns. *C. unifasciata* was mainly active in autumn, *H. itala* in spring. The year-round activity of both species seemed to be related to the amount of rain on the preceding days. Juvenile and adult individuals of *H. itala* differed in their seasonal activity patterns. A larger proportion of juveniles were active during the hot months of the year (June to Mid-August). No difference in seasonal activity between juveniles and adults was found in *C. unifasciata*. In *H. itala*, the highest mortality rates occurred in autumn and winter. In *C. unifasciata*, mortality was not restricted to a particular period of the year.

Kurzfassung. **Tages- und jahreszeitliche Aktivitätsmuster der Landschnecken *Candidula unifasciata* und *Helicella itala* in Magerwiesen des Schweizer Jura (Gastropoda: Stylommatophora: Helicidae).** - Die tages- und jahreszeitlichen Aktivitätsmuster der Gehäuseschnecken *Candidula unifasciata* und *Helicella itala* wurden in Magerwiesen des Nordwestschweizer Jura untersucht. Bei *H. itala* wurden innerhalb einer Periode von 24 Stunden zwei Aktivitätshöhepunkte festgestellt, einer um Mitternacht, der andere nach Tagesanbruch. *C. unifasciata* zeigte nur ein Aktivitätsmaximum um Mitternacht. Die 24-Stunden-Aktivität beider Arten war negativ mit der Lufttemperatur korreliert. Die beiden Arten zeigten Unterschiede bezüglich ihrer saisonalen Aktivität: *C. unifasciata* war vor allem im Herbst aktiv, *H. itala* hingegen im Frühling. Die Jahres-Aktivitätsmuster scheinen bei beiden Arten mit der Regenmenge zusammenzuhängen, die in den Tagen vor der jeweiligen Aufnahme fiel. Juvenile und ausgewachsene Tiere von *H. itala* waren zu verschiedenen Jahreszeiten besonders aktiv. Während der heißen Sommermonate (Juni bis Mitte August) waren mehr Juvenile als Adulte aktiv. Juvenile und ausgewachsene Tiere von *C. unifasciata* zeigten keinen Unterschied in bezug auf ihre saisonale Aktivität. Während *H. itala* die höchsten Mortalitätsraten im Herbst und Winter aufwies, war die Mortalität bei *C. unifasciata* während des ganzen Jahres relativ konstant.

Introduction

Terrestrial gastropods are highly susceptible to desiccation (RUNHAM & HUNTER, 1970; COOK, 1981; BURTON, 1983). For example, active slugs can loose 30-40 % of their body

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weight within 2 h through water loss (DAINTON, 1954). Nevertheless, a variety of terrestrial gastropods occur in dry places such as deserts and dry grasslands (YOM-TOV, 1971; MCQUAID et al., 1979; LIVSHITS, 1985; ARAD et al., 1989; HELLER & ITTIEL, 1990; LAZARIDOU-DIMITRIADOU, 1995). These species have to cope with extreme fluctuations of air temperature and low annual precipitation. Snails have become adapted to these conditions both morphologically (e.g. lighter coloured and thicker shells) and in their behaviour (e.g. restricted activity with aestivation during the warmest period of the year) (MCQUAID et al., 1979; HELLER, 1982; ARAD et al., 1989; HELLER & ITTIEL, 1990).

Activity in terrestrial gastropods has been examined in relation to a variety of climatic parameters (CRAWFORD-SIDEBOTHAM, 1972; BAKER, 1973; DE SMET, 1985; FORD & COOK, 1987; COOK & FORD, 1989; ROLLO, 1991). WEBLEY (1964) estimated that the average night temperature could account for up to 80 % of the variation in day to day numbers of different slugs (*Agriolimax reticulatus, Arion ater, A. fasciatus* and *Milax budapestensis*) caught by baits. WEBLEY (1964) and DAINTON (1943; 1954) showed that temperature had a major influence on slug activity, while no correlation between activity and relative humidity was found. By contrast, activity in the slug *Milax budapestensis* was related to both temperature and relative humidity (CRAWFORD-SIDEBOTHAM, 1972). Furthermore, temperature and humidity initiate activity in *Agriolimax reticulatus* (BAKER, 1973). The activity of *Cochlicella acuta, C. ventricosa, Mesodon normalis* and *Triodopsis albolabris* was light- and temperature-dependent under laboratory conditions (DE SMET, 1985; ASAMI, 1993).

In the present study, I examined the activity patterns of two coexisting land snails, *Helicella itala* (LINNAEUS, 1758) and *Candidula unifasciata* (POIRET, 1801), in calcareous, dry grasslands of the Swiss Jura mountains during single days and over a period of one year. In particular, I addressed the following questions: (1) Do individuals of the two snail species differ in their circadian activity? (2) Do the snail species differ in their seasonal activity patterns? (3) Is activity correlated with environmental parameters such as air temperature, precipitation or relative humidity? (4) Are there differences in seasonal activity between juvenile and adult individuals of *H. itala*?

The temporal distribution of empty shells over a period of a year might give indications of the life cycle of the species. Thus, I also collected empty shells (snails that died during the week preceding the observation) at weekly intervals in defined plots over a period of one year.

Materials and methods

The species

Helicella itala lives in dry, exposed habitats such as calcareous grasslands and dunes. The species is patchily distributed in Western Europe (KERNEY et al., 1983). The relatively flat shell is white with a variable number of dark brown bands. Animals finish shell growth when they reach sexual maturity, but build no distinct lip at the edge of the shell aperture (KERNEY et al., 1983). Adults reach a maximum shell diameter of 15 mm in the northwestern Jura mountains (Switzerland). *Helicella itala* is threatened in Switzerland (TURNER et al., 1994), but very little is known about its life history.

Candidula unifasciata inhabits dry grasslands, rocky heathlands and dunes. It is found in Western Europe with the exception of the British Isles (KERNEY et al., 1983). The shell of *C. unifasciata* is more globular. Its colour is white with a spiral band. Banding variants can occur, and in some snails banding is absent. Adults of *C. unifasciata* reach a shell diameter of up to 7 mm in the populations considered in this study.

Fig. 1: Map indicating the location of the study sites in the Swiss Jura mountains.

Study sites

Activity patterns of *H. itala* and *C. unifasciata* were assessed at three different sites in the Swiss Jura mountains. Site A was located 1 km east of the village of Blauen (47°27' N; 7°32' E) at an elevation of 600 m a.s.l. Sites B and C were located near the village of Nenzlingen (47°27' N; 7°34' E), 2.6 and 3.1 km SE of site A, at an elevation of 520 m a.s.l. (Fig. 1). All sites were on SW facing slopes and are nutrient-poor, dry calcareous grasslands belonging to the Teucrio-Mesobrometum type. For detailed information on plant composition see BAUR et al. (1996). All study sites were grazed by cattle for about three months during summer (June - August).

Recording of circadian snail activity

Activity patterns of *C. unifasciata* and *H. itala* were assessed over 24 hours at two places near site B. The species were observed in areas where they occurred allopatrically to exclude any potentially confounding effects of interspecific competition on activity. The activity of 31 individuals of *C. unifasciata* was recorded one 24 hr clock on 23/24 May 1996 in plots of 2 × 2 m. From 4 p.m. to 3 p.m. on 25/26 September 1996, the activity of 32 individuals of *C. unifasciata* and 28 individuals of *H. itala* was recorded. The circadian activity was recorded on these dates because both species are most active in spring and autumn (see results). All animals were individually marked, at the site, with numbers written in Indian ink on the shell, and released immediately in groups of eight within one meter of the place where they were found. Previous experiments showed that crowding had no influence on the dispersal patterns of *H. itala* (OGGIER, 1994). At intervals of 1 h, the plots were carefully searched for marked animals and their activity was assigned to one of the three classes: not active, softbody partly extended or softbody fully extended. At the same time air temperature and relative humidity at ground level were measured using a Vaisala humidity and temperature indicator HMI 31.

Recording of year-round snail activity

At each of the three sites, four plots, each measuring 2 × 2 m, were permanently marked by putting plastic tubes into the ground at each corner. Interplot distances ranged from 7 to 10 meters. At weekly intervals from October 1993 to October 1994, each of the 12 plots was carefully searched for snails for 4 minutes between 7 and 10 a.m. Animals of both species were recorded as active, inactive or dead. Snails were considered active when their soft body was at least partly extended.

To examine whether activity in *H. itala* is size-dependent, I assigned all living snails into two groups (shell diameter ≤ 7 mm, hereafter referred to as small snails, and shell diameter > 7 mm, hereafter called large snails). The shells of dead snails were also collected at weekly intervals. The diameter of empty shells was measured to the nearest 0.05 mm using vernier callipers.

At each site, air temperature was measured 30 cm above ground level during the 4 minutes searching time (accuracy 0.5 °C). Data on the amount of precipitation were obtained from the nearby meteorological station of Grellingen (1.2 km SE of site C). In addition, cloud cover and substrate humidity were estimated using semi-qualitative scales. The categories for cloud cover were: no clouds, hazy, overcast, fog, light and heavy cloud cover. Substrate humidity was classified as dry with fissures, dry, slightly moist, moist (field capacity), wet (water saturated) and frozen. However, cloud cover and substrate humidity were highly correlated with the amount of precipitation in the two previous days before recording snail activity and with air temperature, respectively (Spearman rank correlation: cloud cover - amount of precipitation in the two previous days, range of r_S at the three sites: 0.53 - 0.57, $n = 52$, in all three cases $p < 0.0002$; substrate humidity - air temperature, range of r_S: 0.50 - 0.75, $n = 52$, in all three cases $p < 0.0004$).

Results

Differences among sites in abundance and activity of snails

The three sites differed in the proportions of *C. unifasciata* and *H. itala*. *Helicella itala* was present at all three sites. *Candidula unifasciata* was the dominant snail species at the sites A and C (76.8 % and 70.9 %, respectively), but no living specimens were observed at site B (only 11 empty shells over one year).

The relative abundance of active and inactive *C. unifasciata* was almost twice as high at site A (10.3 individuals per observation period) than at site C (6.5 individuals). In *H. itala*, most animals were recorded at site B (20.5 individuals per observation period), and relatively few at sites A and C (2.9 and 3.0 individuals per observation period, respectively).

Circadian activity patterns

In *C. unifasciata* and *H. itala*, animals became active at sunset (Fig. 2). The highest proportion of snails were active around midnight; later, the activity decreased. A second, smaller peak of activity occurred after dawn. This bimodal distribution of activity was more pronounced in *H. itala* than in *C. unifasciata*.

On both nights, the proportion of active *C. unifasciata* was positively correlated with air humidity (night in May: $r = 0.90$, $n = 24$, $p < 0.0001$; night in September: $r = 0.72$, $n = 24$, $p < 0.0001$), and negatively correlated with air temperature (May: $r = -0.79$, $n = 24$, $p < 0.0001$; September: $r = -0.71$, $n = 24$, $p < 0.0001$).

In *H. itala*, in which activity was recorded during one night in September, activity was negatively correlated with air temperature ($r = -0.62$, $n = 24$, $p = 0.0009$), but no correlation was found with air humidity ($r = 0.24$, $n = 24$, $p = 0.26$). Thus, the circadian activity of both species was negatively correlated with air temperature.

Year-round activity patterns

Considering the entire one year study period, the sites A and C differed in the proportions of active and inactive *C. unifasciata* (site A: 32.2 % active animals; site C: 58.3 % active snails) ($\chi^2 = 57.56$, d.f. = 1, $p < 0.0001$). Sites with *H. itala* did not differ in the proportions of active and inactive snails ($\chi^2 = 5.84$, d.f. = 2, $p = 0.054$).

The two species differed in their seasonal activity patterns (Fig. 3; $\chi^2 = 424.59$, d.f. = 21, $p < 0.0001$). The main activity season of *C. unifasciata* was in autumn (from the end of August to the beginning of October), whereas *H. itala* was most active in spring (February to May) with a minor peak of activity in autumn (Fig. 3). The largest number of inactive *C. unifasciata* were recorded in autumn and the largest number of inactive *H. itala* in spring (data from periods of two weeks combined $\chi^2 = 409.49$, d.f. = 23, $p < 0.0001$). For a detailed list of the number of animals found on each sampling occasion see table 1.

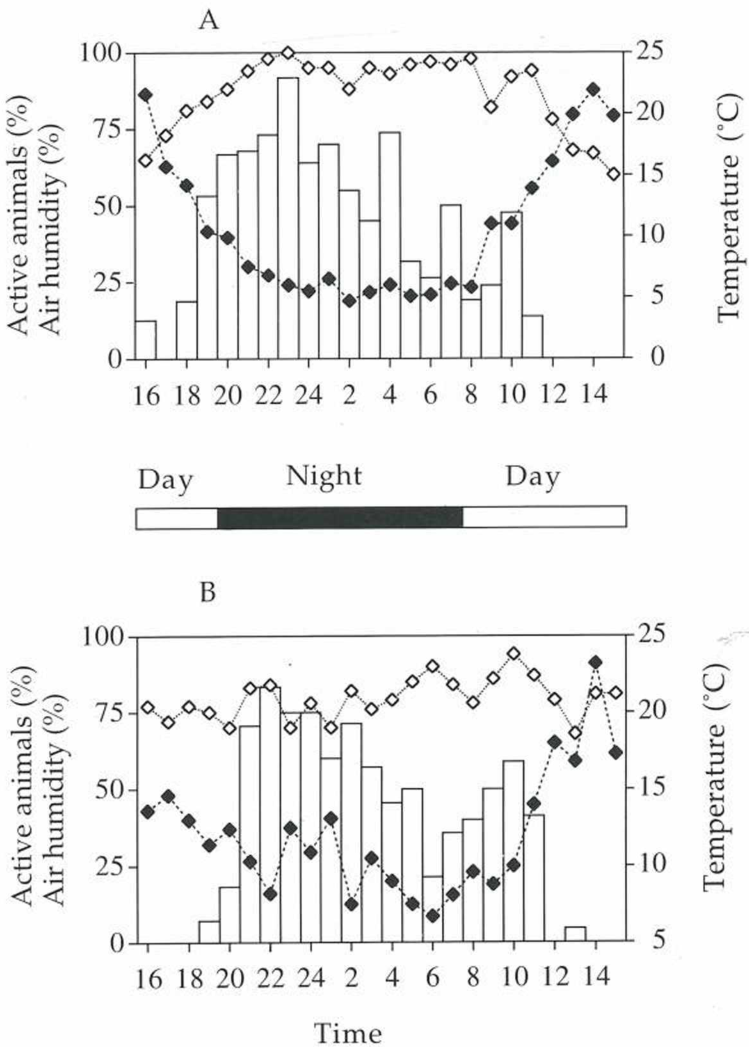

Fig. 2: Circadian activity patterns of *C. unifasciata* (A) and *H. itala* (B) on 25/26 September 1996 in relation to air humidity (◊) and temperature (♦).

In *C. unifasciata*, the number of active animals was positively correlated with the amount of precipitation in the two previous days (site A: $r = 0.47$, $n = 52$, $p = 0.0003$; site C: $r = 0.39$, $n = 52$, $p = 0.0038$; Fig. 3). The proportion of inactive *C. unifasciata* was positively correlated with air temperature (site A: $r = 0.41$, $n = 52$, $p = 0.0021$; site C: $r = 0.44$, $n = 52$, $p = 0.001$).

In *H. itala*, the number of active snails was positively correlated with the amount of precipitation in the two previous days at two of the three sites (site A: $r = 0.34$, $n = 52$, $p = 0.0134$; site B: $r = 0.55$, $n = 52$, $p < 0.0001$; site C: $r = 0.05$, $n = 52$, $p = 0.73$). However, no correlation between the number of active *H. itala* and air temperature was found. Thus, the activity of both snail species seems to be related to the amount of rain in the preceding days. Small and large individuals of *H. itala* differed in their seasonal activity patterns (χ^2 =

Table 1: Number of animals found inactive, active or dead on each sampling occasion over the period of one year. The data of the three study sites was pooled. The dead animals of the first sampling occasion were not included in the analysis.

	Candidula unifasciata			*Helicella itala*		
date	inactiv	active	dead	inactiv	active	dead
28.10. 93	19	0	40	24	1	36
4.11. 93	27	9	19	9	2	11
11.11. 93	14	12	5	7	4	4
18.11. 93	14	0	6	10	0	4
25.11. 93	1	0	10	9	1	5
2.12. 93	0	0	2	0	0	1
9.12. 93	2	3	15	8	4	10
16.12. 93	0	1	8	2	4	6
23.12. 93	0	0	2	3	2	13
30.12. 93	3	9	6	3	9	6
6. 1. 94	6	6	18	1	6	6
13. 1. 94	11	4	18	9	1	17
20. 1. 94	0	0	0	0	0	0
27. 1. 94	3	2	24	13	17	5
3. 2. 94	13	6	12	9	10	2
10. 2. 94	2	6	11	3	26	8
17. 2. 94	1	0	1	0	4	1
24. 2. 94	1	8	12	0	44	4
3. 3. 94	11	4	8	56	10	2
10. 3. 94	0	4	6	2	75	7
17. 3. 94	1	2	6	13	49	3
24. 3. 94	5	0	8	74	15	5
31. 3. 94	8	2	5	68	2	7
7. 4. 94	1	1	3	28	32	2
14. 4. 94	3	9	2	22	73	4
21. 4. 94	2	5	2	13	55	3
28. 4. 94	2	2	3	19	13	0
5. 5. 94	0	4	3	12	34	7
12. 5. 94	0	0	0	18	33	3
19. 5. 94	1	0	2	22	14	4
26. 5. 94	1	0	3	8	9	2
2. 6. 94	0	0	0	1	9	0
9. 6. 94	3	3	0	30	21	3
16. 6. 94	1	1	0	5	1	5
23. 6. 94	3	0	2	18	0	4
30. 6. 94	13	0	2	5	2	4
6. 7. 94	29	1	2	8	0	1
14. 7. 94	44	0	0	23	0	1
21. 7. 94	20	18	6	11	6	4
28. 7. 94	16	0	3	24	0	3
4. 8. 94	84	3	2	46	4	0
11. 8. 94	11	10	4	6	25	2
18. 8. 94	14	26	13	4	10	0
25. 8. 94	9	5	12	4	6	5
1. 9. 94	36	52	12	3	13	7
8. 9. 94	23	46	5	0	18	4
15. 9. 94	20	21	6	10	6	5
22. 9. 94	8	44	5	1	16	4
29. 9. 94	11	18	4	2	3	1
6.10. 94	6	7	14	0	9	2
13.10. 94	2	6	15	0	3	2
20.10. 94	0	10	4	2	8	3

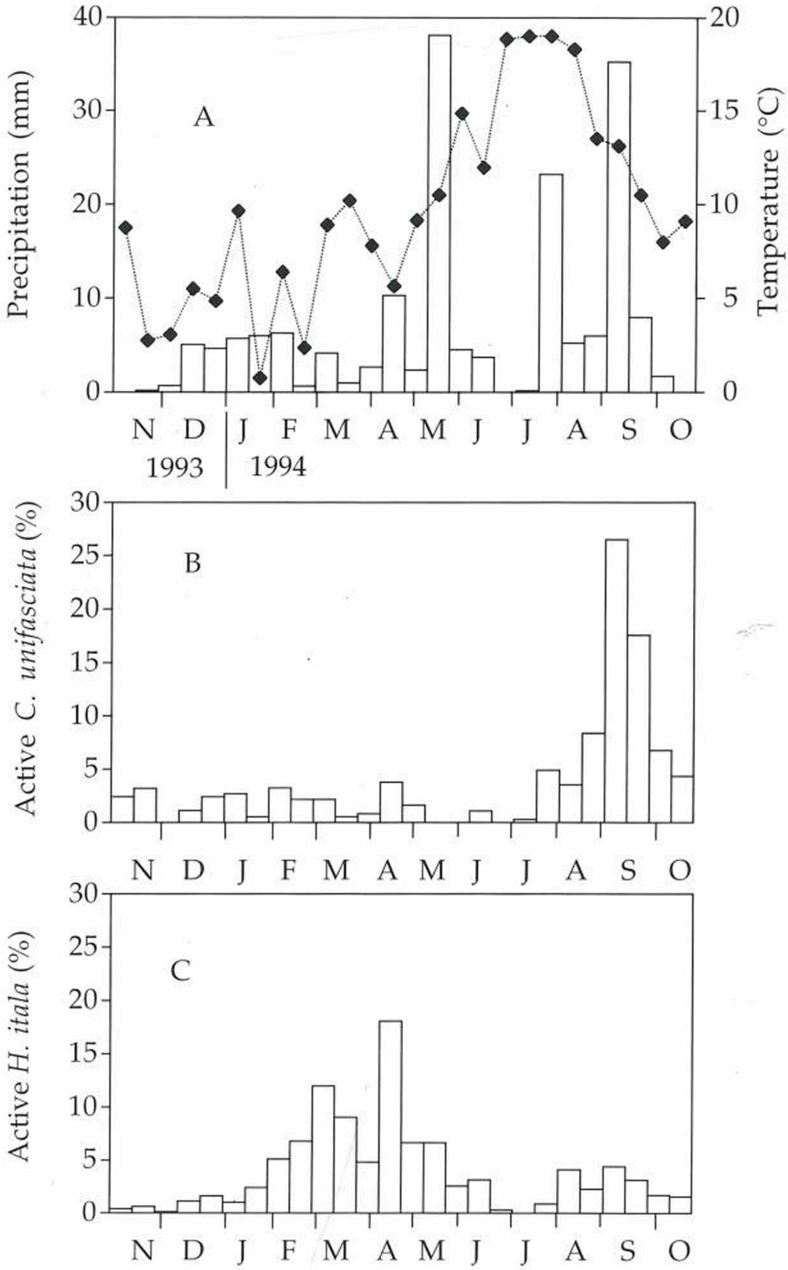

Fig. 3 A): Seasonal variation in air temperature (♦) and the amount of precipitation of the two preceding days (bars). B): Percentage of active *C. unifasciata* and (C) *H. itala* over one year. All active animals found in the course of one year represent 100 %. Each bar represents the combined data of two consecutive weeks (i.e. two records), and all sites.

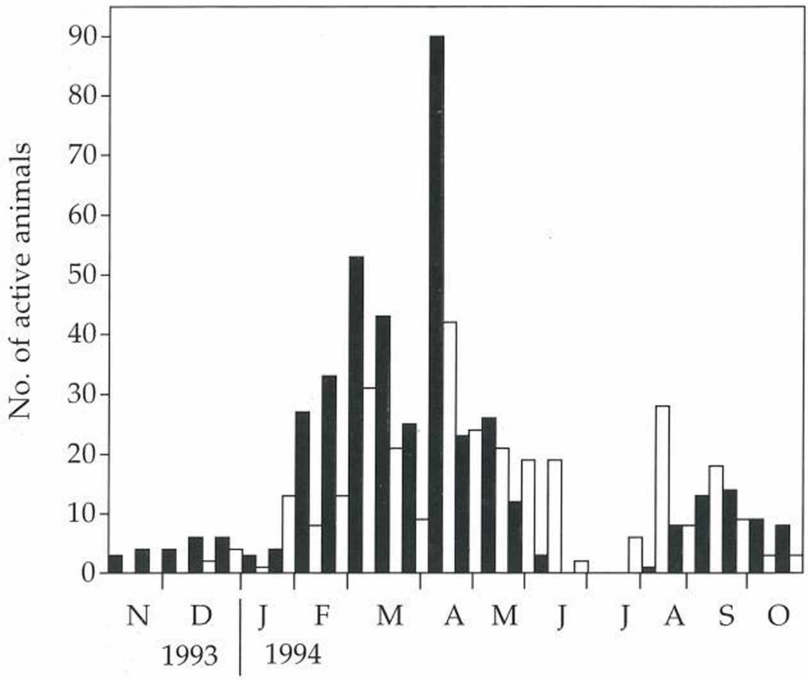

Fig. 4: Circannual activity patterns of small (white bars) and large (black bars) individuals of *H. itala*. Each bar represents the combined data of two consecutive weeks (i.e. two records), and all sites.

114.48, d.f. = 18, $p < 0.0001$; Fig. 4). Furthermore, small and large snails differed in the proportion of inactive individuals observed ($\chi^2 = 211.31$, d.f. = 21, $p < 0.0001$). The highest proportion of small individuals (active and inactive) were recorded between June and Mid-August. This means that a larger proportion of small individuals was observed in the dry and hot months. Correlations between the activity of the two size classes and environmental parameters (air temperature and amount of precipitation in the two previous days) showed no difference between large and small snails.

Change of mortality over the year

The temporal distribution of empty shells may provide insight into seasonal changes of mortality rates of the two snail species in the investigation area. Figure 5 shows the number of empty shells of both species. The frequency distribution of dead animals collected at intervals of two weeks differed significantly between the two species ($\chi^2 = 42.04$, d.f. = 20, $p = 0.0027$).

In *C. unifasciata*, the number of dead individuals (empty shells) found exceeded 11 animals per 14 days at most sampling occasions, except in the period from April to August. In *H. itala*, the number of dead snails found was low throughout spring and summer (exceeding 11 animals only once in September). However, it increased steadily from November onwards and reached a maximum in January. Thus, in *H. itala*, the highest mortality rates occurred in winter.

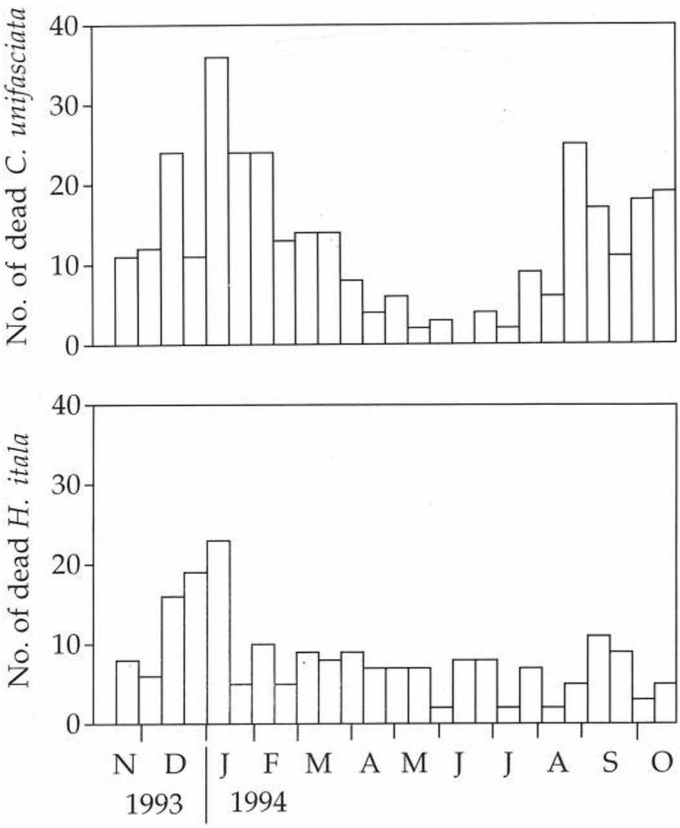

Fig. 5: Number of empty shells (dead animals) collected in the course of one year. Each bar shows the number of shells collected over two weeks.

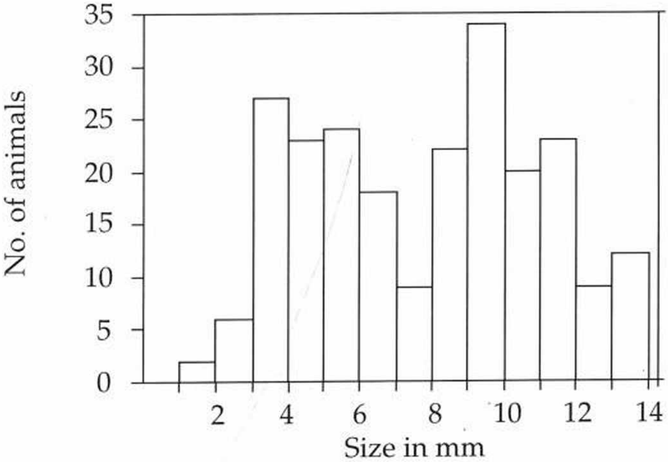

Fig. 6: Frequency distribution of the diameter of empty shells of *H. itala* found in the course of one year.

In *H. itala*, the frequency distributions of empty shells collected in two-week intervals differed significantly between small and large snails ($\chi^2 = 45.57$, d.f. = 15, $p < 0.0001$). In spring, more small dead snails were found, whereas in autumn and winter large dead animals were more frequently encountered.
In *H. itala*, the proportion of small shells decreased from spring to winter (59.7 % in spring, 45.5 % in summer, 42.5 % in autumn and 37.7 % in winter). This suggests that *H. itala* may reproduce early in spring and that many newly hatched snails die. The frequency distribution of the diameter of empty shells in *H. itala* was bimodal when data over 12 months were combined (Fig. 6). The number of empty shells of *C. unifasciata* showed no such bimodal distribution.

Discussion

At both sites where the species coexisted, *C. unifasciata* occured in much higher numbers. Assuming that the same area can support more individuals of the smaller *C. unifasciata* than of the larger *H. itala*, the reason for this could simply be the difference in body size. However, at site B, were *C. unifasciata* was absent, the number of *H. itala* was four to five times higher than at the sites A and C where the species coexist. This could either be a result of interspecific competition or of small-scaled differences in habitat quality. The present study does not distinguish between these alternative explanations.
The number of animals of each species also differed between the plots of the same site, i.e. at a scale of 10-20 m. These differences among plots remained constant throughout the seasons. Possible explanations for the intrasite differences in population density may include heterogeneity in microclimatic conditions, food plants and shelter sites, but not be due to a limited dispersal ability of the snails. Field experiments showed that *H. itala* is able to move up to 6.4 m in one week or 10.2 m in two weeks and thus can travel much farther than the distance between two plots of the present study (OGGIER, 1994).

In the circadian activity patterns, falling temperatures may have induced activity in both species. The same is found for the slugs *Deroceras reticulatum* (DAINTON, 1954; BAKER, 1973) and *Arion ater* (DAINTON & WRIGHT, 1985; FORD & COOK, 1987). FORD & COOK (1987) showed that *Limax pseudoflavus* exhibited bursts of crawling after a temperature reduction to 4 °C. However, they argued that the conclusions drawn by DAINTON & WRIGHT (1985) might not be relevant under natural conditions as all their experiments were conducted in the laboratory during daytime when the animals would normally be inactive. *Cochlicella ventricosa* became more active with rising temperature, whereas the activity of *Cochlicella acuta* increased from 1 °C to 10 °C and then decreased with further rising temperature (DE SMET, 1985). Thus, temperature might be an important factor inducing activity in many land snails.
To minimize the effect of time of day, we visited the field sites for the year-round activity experiment at the same time of day every week. However, the present study shows that between 7 and 10 a.m. 19.0 % to 50.0 % of the animals in *C. unifasciata* and 35.7 % to 58.8 % in *H. itala* were active. These fluctuations could partly be due to differences in weather conditions. As the main activity peak of both species is around midnight, the snails may be particularly sensitive to unfavorable weather early in the morning, resulting in these fluctuations.

The bimodal distribution of circadian activity was more pronounced in *H. itala* than in *C. unifasciata*. Bimodal circadian activity patterns are also known for the snails *Cepaea nemoralis, C. hortensis, Arianta arbustorum* (CAMERON, 1970), *Cochlicella acuta* and *C. ventricosa* (DE SMET, 1985), *Mesodon normalis* (ASAMI, 1993) and *Helix aspersa maxima* (BLANC, 1993). On the other hand, the snails *Helix aspersa* (BAILEY, 1975; BAILEY, 1981), and

Triodopsis albolabris (ASAMI, 1993) exhibited unimodal circadian activity patterns. Unimodal circadian activity patterns have been documented in the slugs *Limax maximus* (SOKOLOVE et al., 1977), *Limax pseudoflavus* (COOK, 1981; FORD & COOK, 1987) and *Deroceras reticulatum* (ROLLO, 1991). Although these studies cannot be directly compared with each other, there seems to be a tendency that slugs have unimodal and snails bimodal circadian activity patterns. This could be due to the fact that slugs suffer more from desiccation and, thus, avoid being active early in the morning when temperature and light conditions can rapidly change.

The year-round activity patterns differed between the two species. The main activity peak of *C. unifasciata* was in autumn. At this time of year the snails mate and lay their eggs (a copulating pair was observed on 8 September 1993). In *H. itala*, the only copulation observed was in December and an individual with extended copulatory organs was recorded in November. Eggs were found between January and May and again in October. Although it was impossible to distinguish the eggs of the two species in the field, activity patterns and field observations showed that at least *H. itala* is able to reproduce both in spring and autumn (OGGIER, unpublished data). *H. itala* maintained its activity patterns whether it occurred alone (at site B) or together with *C. unifasciata*. This suggests that the differences in seasonality are not due to the direct interactions of the species but rather a consequence of evolutionary divergence as in *Cepaea* (CAMERON, 1970; TILLING, 1986; COWIE & JONES, 1987).

The correlations with environmental parameters over one year showed that the activity in both species depended on the amount of rain in the two preceding days. Many studies show that relative humidity is a key factor for activity (LEWIS, 1969; CRAWFORD-SIDEBOTHAM, 1972; BAKER, 1973). Relative humidity may be correlated with rainfall in dry grasslands. In fact, the records of the 24-hour activity study indicate that relative humidity is a key factor for stimulating activity, at least in *C. unifasciata*.

This study shows that *H. itala* is active throughout winter as long as there is no snow cover, and that activity is interrupted during summer by aestivation. It was surprising to record significantly more small than large *H. itala* during the hottest and driest months of the year. The reason for this could be a higher desiccation rate in small animals which could force them to search for water and food and would result in more and/or longer active phases, as demonstrated in the slug *L. maximus* (HESS & PRIOR, 1985). When the slugs were transferred from wet to dry activity wheels, the intensity and duration of locomotor activity increased. An alternative explanation is given for *T. pisana* by COWIE (1985). In this species, juveniles are more tolerant to high temperatures than adults, probably because of their greater ability to use evaporation cooling for short periods.
The frequency distribution of the diameter of empty shells in *H. itala* was bimodal when data over 12 months were combined. This sharp separation between juveniles and adults with almost no intermediates has also been observed in undisturbed populations of *Helix texta* (HELLER & ITTIEL, 1990). It could be an indication of some kind of control of the juvenile growth rate by the adult animals or of a very high mortality rate among the juveniles.

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