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Snail Populations, Beech Litter Production, and the Role of Snails in Litter Decomposition

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Summary. The population densities of snails living in beech litter were studied form March 1968 to April 1969. Litter production over one year was measured and the role of snails in litter disappearance assessed.

Snails were extracted from litter using a modified Vágvölgyi (1952) flotation method, extraction efficiencies being 84%. The mean annual population density of the twenty-one species of snail recorded on the main sampling site was estimated at 489/m². *Carychium tridentatum* was the most numerous species, with a mean density of 200/m². *Acanthinula aculeata*, *Punctum pygmaeum* and *Vitrea contracta* also had fairly high mean densities. The mean annual biomass was 699 mg dry wt./m² or 278 mg ash-free dry wt./m². *Hygromia striolata* and *Oxychilus cellarius/alliarius* were the most important species in terms of biomass on the main site. Within the limits of accuracy imposed by the sampling regime the population densities of four out of five of the species (*C. tridentatum*, *A. aculeata*, *V. contracta*, *Retinella pura*) studied remained unchanged throughout the year, whereas *P. pygmaeum* had a significantly higher autumn population. *C. tridentatum* populations were highly aggregated at all times of the year, most markedly so in June. Other species were aggregated at certain times of the year only. Samples taken from other sites showed total population densities of snails ranging from 185—1082 snails/m².

A total tree litter production of 652 g/m²/annum was recorded, of which 584 g/m²/annum was of beech material. 72% fell in the October-December period. 58% of the beech litter-fall was leaves, 5.2% bud-scales, 27% fruits and 10% twigs and bark. Summation of appropriate field layer peak standing crops amounted to 23.3 g/m². This was considered as potential litter and was equivalent to 3.4% of the total litter input. The litter standing on the woodland floor in September 1968 was 2,700 g/m², hence, assuming a steady state, litter turnover time was estimated as 4.5 years.

It was calculated that the total snail population ingested 0.35—0.43% of the annual litter input, of which 49% was assimilated. The role of the individual species is examined in relation to concepts of "key species" in ecosystem functioning. The possible role of slugs in decomposition processes is also discussed.

Introduction

Despite the suggestion that land molluscs may be of importance in the functioning of some terrestrial ecosystems (Lindquist, 1941; Fröm-

ming, 1958) few population studies have been made, possibly because mollusc sampling and extraction methods have proved difficult.

The present paper reports on the population density and biomass of snails dwelling in beech litter from March 1968 to April 1969. Details of litter production during the year beginning July 1968 are also given and the impact of the snail population on litter removal calculated.

Site

The study was made in Wytham Woods, near Oxford (latitude 51° 46′ N, longitude 1° 20′ E) at an altitude of 152 m. The chief experimental site (Site 1, Singing Way) consisted of thirteen beeches *Fagus sylvatica* L., planted between 1814 and 1827 on the crown of a hill. To the north-east of Site 1 was a large, arable field and to the south, on the slope of the hill, a conifer plantation. To the west, north-west and east was mixed woodland of oak *Quercus robur* L., ash *Fraxinus excelsior* L., sycamore *Acer pseudoplatanus* L., hornbeam *Carpinus betulus* L., sweet chestnut *Castanea sativa* Mill. and birch *Betula pendula* Roth. The beech stand was exposed to south-westerly gales.

Site 1 had a patchy and sparse field layer, consisting chiefly of dog's mercury *Mercurialis perennis* L., with lesser amounts of enchanter's nightshade *Circaea lutetiana* L., violet *Viola reichenbachiana* Bor., hawthorn *Crataegus monogyna* Jacq., privet *Ligustrum vulgare* L., herb robert *Geranium robertianum* L., goose grass *Galium aparine* L., wood avens *Geum urbanum* L., nettle *Urtica dioica* L., bramble *Rubus fruticosus* agg., soft grass *Holcus mollis* L. and seedlings of *Acer pseudoplatanus*, *Fagus sylvatica* and *Fraxinus excelsior*.

The soil of Site 1 was a shallow rendzina (depth 13—20 cm, pH 7.0—7.5) overlying a bedrock of Corallian limestone. Precipitation during the period March 1968 to February 1969 amounted to 886 mm, 344 mm during the period 1st July to 30th September. A mean annual air temperature of 8.5° C was recorded (mean maximum 11.1° C, mean minimum 5.6° C); however, the December and February mean monthly minima fell below zero.

Comparative samples were taken from three further sites in Wytham Woods. Site 2 (Beech Grove) was a beech woodland of similar age, on similar soil, to Site 1, but with a more luxurious field layer, chiefly of *Mercurialis perennis*, and in places a well-developed shrub-layer of *Rubus fruticosus* agg. and hazel *Corylus avellana* L. Site 3 (Brogden's Belt) resembled Sites 1 and 2, but with a very sparse field layer and no shrub layer; the litter was thin owing to wind-blow. The oak-ash-sycamore woodland of Site 4 (Chalet) was on a brown earth soil. There was a thick field layer of *Mercurialis perennis* and *Rubus fruticosus*, with a rich bryophyte carpet; the litter was very thin or absent on the June sampling date.

Methods

A grid was laid out on the woodland floor of Site 1, and consisted of two parallel rows of five 10 m squares, the rows being 10 m apart. A further row of seven 10 m squares was laid out on the opposite side of a path traversing the site. Alternate 10 m squares (ten in all) were used for sampling molluscs, the squares in between being used for litter collection. The sampling squares were further marked with stakes along the edges at 2 m intervals, so that they could be readily divided by eye into 1 m units.

Sampling and Extracting the Snails. On each of thirteen sampling occasions thirty 12 cm diameter samples were taken, three from each 10 m square. The sampling positions were arrived at by reference to tables of random numbers. Samples, consisting of litter and the top few centimetres of soil, were placed in numbered polythene bags for return to the laboratory. No 1 m unit was sampled twice in the sampling programme and a total of only 0.4% of the litter in the sampling area was removed.

In the laboratory the samples were weighed and snails were extracted using a modified Vágvölgyi (1952) flotation technique. The procedure was as follows:

1) Each sample was put into hot water (60°C) in a white, polythene bowl (35 cm diameter), stirred vigorously several times and left for 30 min to settle. The soil in the sample, and a proportion of litter, sank to the bottom of the bowl, the remaining litter floated. Badly broken shells, and those that were dead and soil-filled, sank. Dead, air-filled shells floated. Living snails were killed by the heat, and being denser than water they sank to the bottom of the bowl. Any snails clinging to the litter were dislodged by heat-shock and stirring, and sank.

2) The floating litter and dead, empty shells were removed from the water-surface and discarded. A search of the water-surface was made under strong light to ensure that all floating shells had been removed.

3) The water, containing the sunken material, was passed through a fine sieve (mesh size 0.3 mm) and the retained material was placed in an aluminium container and oven-dried at 120°C for sixteen hours.

4) The dried material was carefully crumbled into a solution of dodecylbenzene sulphonic acid sodium salt (4 g/l) in a white, polythene bowl; the detergent acted as a wetting agent. Most plant material sank, as did badly broken and soil-filled shells. The "live" snails had become air-filled during drying and floated; they were collected by searching under a strong light.

The efficiency of extraction was determined by hand sorting ten samples of beech litter and soil to remove snails and introducing ten *Discus rotundatus* Müller (size range 1.5—6.0 mm) into each sample. These were left for 24 hours to allow dispersion. The samples were extracted as noted above and an extraction efficiency of 84% was calculated.

For comparative purposes twenty random samples were taken from each of the Sites 2, 3 and 4 in May and June 1969.

Biomass Determination. The collected shells were measured using an eye-piece micrometer. With spire shells (e.g. *Marpessa, Carychium*) shell height was measured. With helicoid shells (e.g. *Discus, Hygromia*) the maximum diameter, measured from the aperture, was taken.

The relationships between shell measurements and weight were determined in order to convert numbers into biomass. Animals of a range of sizes were measured, blotted to remove surface water and dirt, and weighed alive. Large animals were weighed on a Sartorius model 2604 balance, small animals on an EMB-1 electric micro-balance. The animals were then dried in a vacuum oven at 60°C for two days, and their dry weight determined. As shells are metabolically inactive, it was considered necessary to determine the biomass of living tissue and so the dried snails were ashed in a mufflefurnace at 600°C for two days and their ash-free dry weight calculated by difference between ash-weight and dry weight.

Measurement of Tree Litter Production. Twenty litter traps were erected in a stratified random manner on the 10 m squares not used for sampling snails. The trap design followed that of Ovington and Murray (1964), and consisted of a metal hoop of 50 cm diameter, from which a weighted sail-cloth bag of 1 m depth was suspended. Traps were placed in position on 30th June 1968 and emptied at the

beginning of each subsequent month. Following Newbould (1967) collected material was divided into leaves, bud-scales and flowers, twigs and bark, fruits, and detritus (dead invertebrates, faeces and a small amount of inorganic matter). Samples were oven-dried to constant weight at 60° C.

Measurement of Field Layer Standing Crop. The field layer standing crop was determined as a best approximation of potential field layer litter production. Samples were taken on 17th April 1969 (for maximum production of vernal plants e.g. *Viola*) and 20th July 1969 (for maximal production of aestival species e.g. *Mercurialis*). A quadrat of 0.25 m^2 was thrown randomly over the shoulder and twenty-two samples were taken on each occasion. All aboveground parts of the plants were removed. Samples were divided into species and dried to constant weight at 60° C.

Measurement of the Litter Standing Crop. To obtain a measure of litter standing crop before the main leaf-fall, eight samples of 0.25 m^2 were taken on 17th September 1968. Samples were dried to constant weight at 60° C. Four samples were then sorted into the following components: branches and twigs of $>$ 1 cm diameter; twigs of $<$ 1 cm diameter; fruits; and leaves; and the proportions obtained were assumed to apply for the remaining four samples.

Results

Populations of Snails

Twenty-one species of shelled molluscs belonging to eleven families were recorded on Site 1: *Carychium tridentatum* (Risso), *Cochlicopa lubrica* (Müller), *Columella edentula* (Draparnaud), *Pupilla muscorum* (L.), *Vallonia pulchella* (Müller), *Acanthinula aculeata* (Müller), *Ena obscura* (Müller), *Marpessa laminata* (Montagu), *Clausilia bidentata* (Ström), *Vitrea contracta* (Westerlund), *Retinella radiatula* (Alder), *Retinella pura* (Alder), *Retinella nitidula* (Draparnaud), *Oxychilus cellarius* (Müller), *Oxychilus alliarius* (Miller), *Euconulus fulvus* (Müller), *Vitrina pellucida* (Müller), *Hygromia striolata* (C. Pfeiffer) and *Hygromia hispida* (L.). *Pomatias elegans* (Müller) and *Cepaea nemoralis* (L.) were found as dead animals only on Site 1. Eleven of the above species were recorded on Site 2, plus *Arianta arbustorum*, and eight of the species were recorded on each of Sites 3 and 4 (see Table 5).

Carychium tridentatum, *Acanthinula aculeata*, *Punctum pygmaeum* and *Vitrea contracta* were common species on all sites. Regressions for conversions from length or width to dry weight and ash-free dry weight were calculated for the fifteen species most easily collected by hand. The equations are given in Table 1. Owing to rarity or small size, insufficient or no data were available for calculating regressions for the remaining seven species. Biomasses of *Columella* and *Arianta* were computed from lines drawn by eye through data on a few specimens only. The biomasses of the other species were determined using the regressions of those species closest in size and shape. The regression data of *Marpessa* was used to calculate *Pupilla* biomass, those of *Discus*

Table 1. *Size/weight relationships of fifteen species of snail*

Species	Dry wt. (y) v. length or width (x)	No. samples	Ash-free dry wt. (y) v. length or width (x)	No. samples
Carychium tridentatum	$\log (y \times 10) = -0.08 + 2.62 \log x$	51	$\log (y \times 100) = 0.29 + 2.63 \log x$	44
Acanthinula aculeata	$\log (y \times 10) = 0.15 + 3.02 \log x$	11	$\log (y \times 10) = -0.26 + 3.24 \log x$	11
Cochlicopa lubrica	$\log (y \times 10) = 0.25 + 2.11 \log x$	12	$\log (y \times 10) = -0.14 + 2.05 \log x$	12
Ena obscura	$\log y = -0.18 + 1.63 \log x$	6	$\log y = -0.50 + 1.59 \log x$	6
Marpessa laminata	$\log y = -0.07 + 2.42 \log x$	28	$\log (y \times 10) = -0.60 + 2.41 \log x$	28
Clausilia bidentata	$\log y = -1.30 + 2.68 \log x$	27	$\log (y \times 10) = -0.50 + 2.37 \log x$	27
Vitrea contracta	$\log (y \times 10) = -2.21 + 2.41 \log (x \times 10)$	30	$\log (y \times 100) = -2.39 + 3.05 \log (x \times 10)$	28
Retinella pura	$\log (y \times 10) = -2.41 + 2.54 \log (x \times 10)$	6	$\log (y \times 10) = -2.94 + 2.68 \log (x \times 10)$	6
Retinella nitidula	$\log y = -0.90 + 2.71 \log x$	16	$\log (y \times 10) = -0.12 + 2.54 \log x$	15
Oxychilus cellarius	$\log y = -0.94 + 2.82 \log x$	24	$\log y = -1.31 + 2.88 \log x$	23
Oxychilus alliarius	$\log y = -1.09 + 2.92 \log x$	28	$\log y = -1.38 + 2.82 \log x$	28
Euconulus fulvus	$\log y = -1.16 + 3.36 \log x$	23	$\log (y \times 10) = -0.61 + 3.57 \log x$	23
Discus rotundatus	$\log y = -0.79 + 2.78 \log x$	45	$\log y = -1.30 + 2.66 \log x$	45
Vitrina pellucida	$\log (y \times 10) = 0.06 + 2.45 \log x$	9	$\log (y \times 10) = -0.18 + 2.58 \log x$	9
Hygromia striolata	$\log y = -0.85 + 2.80 \log x$	25	$\log (y \times 10) = -0.94 + 3.63 \log x$	23

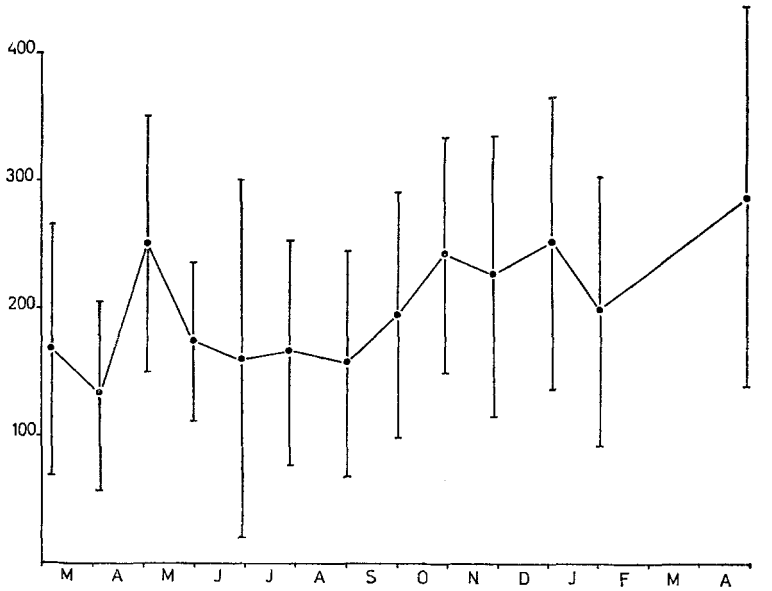
N.B. Data transformed in some instances to avoid the use of negative logs.

were used for computation of the population biomasses of *Vallonia* and *Punctum*; *Retinella radiatula* biomass was determined from data for *R. pura*, and *Hygromia hispida* biomass from data for *H. striolata*. It was found impossible to distinguish young individuals of *Oxychilus cellarius* and *O. alliarius*, so they were treated for biomass determination as a single species; the regression coefficients of the width-weight relationships of adults were very similar (see Table 1).

The mean annual population densities and biomasses of the twenty-one species of snail living on Site 1 are shown in Table 2. Monthly population densities (population/$m^2 \pm$ SE) of the five commoner species, *Carychium tridentatum, Acanthinula aculeata, Punctum pygmaeum, Vitrea contracta* and *Retinella pura* are shown in Figs. 1—5, their monthly biomasses being given in Table 3. As the variance on the population estimates was large, the degree of aggregation in the five common species was examined using the variance: mean ratio, signifcance being determined using a *t*-test (Grieg-Smith, 1964), results are shown in Table 4.

Table 2. *The population density and biomass of twenty-one species of snail living in beech litter (mean of thirteen sampling occasions) at Site 1*

Species	Nos/m^2	Biomass dry wt. (mg/m^2)	Biomass ash-free dry wt. (mg/m^2)
Carychium tridentatum	199.80	65.84	13.31
Cochlicopa lubrica	0.90	3.11	1.15
Columella edentula	3.37	1.88	0.94
Pupilla muscorum	0.67	0.22	0.07
Vallonia pulchella	0.67	0.90	0.25
Acanthinula aculeata	71.49	50.86	22.48
Ena obscura	3.82	52.96	23.45
Marpessa laminata	1.80	9.32	2.70
Clausilia bidentata	0.45	5.50	1.42
Vitrea contracta	39.10	22.06	9.36
Retinella radiatula	0.45	0.86	0.36
Retinella pura	24.71	21.62	10.15
Retinella nitidula	7.86	27.26	12.79
Oxychilus cellarius/alliarius	46.27	160.22	69.55
Euconulus fulvus	1.57	2.02	0.87
Punctum pygmaeum	67.16	19.39	4.17
Discus rotundatus	13.50	89.47	23.32
Vitrina pellucida	1.57	2.14	1.44
Hygromia striolata	8.54	163.66	80.04
Hygromia hispida	0.67	1.39	0.25
Total	488.65	698.91	278.07



Figs. 1—5. The population density of snails in beech litter from March 1968 to April 1969 (nos./m^2 $\pm$ 95% confidence limits)

Fig. 1. *Carychium tridentatum*

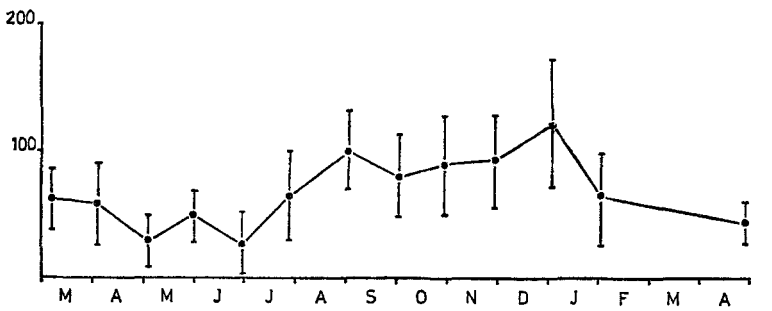


Fig. 2. *Punctum pygmaeum*

The mean annual total population density of snails on Site 1 was 489/m^2. *Carychium tridentatum* was the most numerous species, with a mean density of 200/m^2 over the thirteen sampling occasions. Considered in terms of dry weight biomass *Hygromia striolata* and *Oxychilus cellarius/alliarius* were the most important species on Site 1. *Carychium tridentatum* was only of fourth importance on a dry weight biomass basis and only of sixth importance when considering ash-free dry weight.

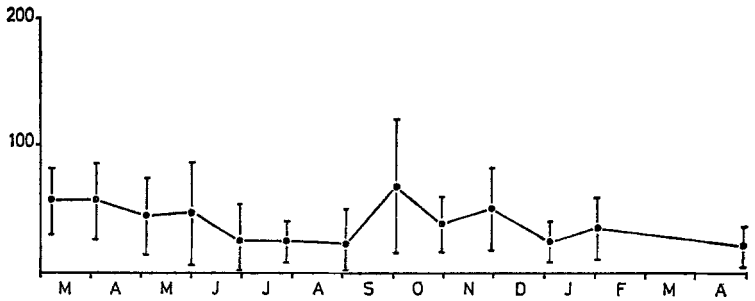


Fig. 3. *Vitrea contracta*

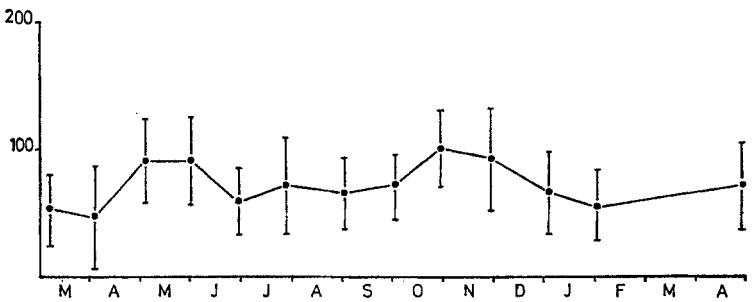


Fig. 4. *Acanthinula aculeata*

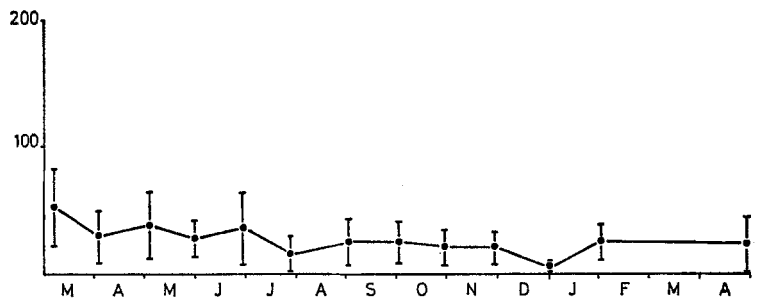


Fig. 5. *Retinella pura*

The population densities of *Carychium tridentatum*, *Vitrea contracta*, *Acanthinula aculeata* and *Retinella pura* were stable, with no significant differences over the sampling period, within the limits of accuracy imposed by the technical problems and time of sorting large numbers

Table 3. *The mean monthly population biomass of five species of snail in beech litter at Site 1*

Date	*Carychium tridentatum*		*Acanthinula aculeata*		*Punctum pygmaeum*		*Vitrea contracta*		*Retinella pura*	
	dry wt. (mg/m^2)	ash-free dry wt. (mg/m^2)	dry wt. (mg/m^2)	ash-free dry wt. (mg/m^2)	dry wt. (mg/m^2)	ash-free dry wt. (mg/m^2)	dry wt. (mg/m^2)	ash-free dry wt. (mg/m^2)	dry wt. (mg/m^2)	ash-free dry wt. (mg/m^2)
12. 3. 68	48.91	9.99	33.70	14.63	19.13	4.44	30.89	12.96	49.29	23.10
9. 4. 68	45.11	9.14	35.10	15.56	16.70	3.71	30.51	12.82	69.17	34.98
7. 5. 68	92.65	18.60	72.04	32.03	9.93	2.45	24.91	10.60	32.35	15.04
31. 5. 68	63.28	12.73	60.06	26.37	15.33	3.50	26.68	11.30	19.18	8.85
29. 6. 68	54.31	10.95	34.08	14.80	8.79	2.22	12.18	5.02	15.91	7.15
25. 7. 68	55.24	11.18	56.74	25.40	18.31	3.85	11.45	5.81	6.80	3.01
4. 9. 68	59.48	11.86	54.52	24.53	24.62	4.29	17.46	6.83	12.18	5.40
2. 10. 68	61.06	12.38	59.25	26.43	19.74	3.50	39.39	16.38	15.88	7.15
29. 10. 68	77.67	15.71	56.74	24.62	23.65	4.73	16.70	6.54	17.75	8.03
27. 11. 68	63.04	12.91	57.96	25.37	26.78	5.78	31.27	13.69	11.10	4.96
7. 1. 69	78.99	16.00	46.84	20.76	36.21	8.00	15.30	6.77	2.60	1.17
3. 2. 69	63.31	12.85	31.89	13.84	18.60	4.26	21.43	9.20	15.74	7.10
28. 4. 69	92.91	18.78	62.25	27.92	14.28	3.47	8.99	3.71	13.05	5.99
Mean	65.84	13.31	50.86	22.48	19.39	4.17	22.06	9.36	21.62	10.15

Table 4. *The variance: mean ratios of samples of five species of snail on thirteen sampling occasions*

Date	*Carychium tridentatum*		*Acanthinula aculeata*		*Punctum pygmaeum*		*Vitrea contracta*		*Retinella pura*	
	σ/m	t	σ/m	t	σ/m	t	σ/m	t	σ/m	t
12. 3. 68	4.03	11.54	1.23	0.88	0.78	0.84	—	—	—	—
9. 4. 68	3.47	9.41	3.00	7.62	1.46	1.75	1.33	1.26	1.08	0.30
7. 5. 68	3.48	9.44	0.94	0.23	1.08	0.30	1.70	2.67	1.51	1.94
31. 5. 68	1.97	3.69	1.11	0.42	1.13	0.50	3.00	7.61	0.70	1.14
29. 6. 68	10.32	35.49	0.93	0.23	1.81	3.08	3.19	8.34	1.93	3.54
25. 7. 68	3.90	11.04	1.80	3.05	1.57	2.17	0.96	0.51	1.20	0.76
4. 9. 68	4.28	12.49	1.01	0.04	0.82	0.69	1.43	1.64	1.21	0.80
2. 10. 68	3.93	11.15	0.70	0.14	1.13	0.50	3.32	8.83	0.96	0.15
29. 10. 68	2.84	7.01	0.82	0.69	1.39	1.49	1.04	0.15	0.78	0.84
27. 11. 68	4.65	13.90	1.51	1.94	1.19	0.72	1.82	3.12	0.77	0.88
7. 1. 69	4.43	13.10	1.36	1.37	1.82	3.12	0.86	0.53	1.08	0.30
3. 2. 69	5.78	18.20	1.22	0.84	1.83	3.16	1.28	1.07	0.72	1.00
28. 4. 69	6.27	20.07	1.33	1.26	0.52	1.83	1.09	0.34	0.93	0.27

$t > 2.76$ for significance at 1% level ($df = 29$).

Table 5. *Population density and biomass of snails on three subsidiary sampling sites*

Species	Site 2			Site 3			Site 4		
	2nd June 1969			21st June 1969			23rd June 1969		
	Nos/m² + SE	dry wt. biomass (mg/m²)	ash-free dry wt. biomass (mg/m²)	Nos/m² + SE	dry wt. biomass (mg/m²)	ash-free dry wt. biomass (mg/m²)	Nos/m² + SE	dry wt. biomass (mg/m²)	ash-free dry wt. biomass (mg/m²)
Carychium tridentatum	751.4 ± 97.2	258.92	52.42	66.3 ± 29.2	24.49	4.95	340.3 ± 76.2	131.94	26.52
Cochlicopa lubrica	4.4 ± 4.4	2.78	1.11	—	—	—	30.9 ± 16.8	71.47	24.84
Acanthinula aculeata	53.0 ± 12.4	31.43	13.66	17.7 ± 8.3	12.16	5.35	26.5 ± 9.7	17.19	7.56
Ena obscura	4.4 ± 4.4	9.77	4.29	4.4 ± 4.4	97.42	42.79	—	—	—
Vitrea contracta	106.1 ± 32.7	62.54	27.18	30.9 ± 18.6	17.86	7.38	35.4 ± 15.0	35.45	17.77
Retinella pura	44.2 ± 15.0	38.94	18.52	—	—	—	—	—	—
Oxychilus cellarius/ alliarius	13.3 ± 9.7	50.34	22.01	22.1 ± 11.2	26.39	12.24	17.7 ± 10.6	13.66	6.41
Euconulus fulvus	17.7 ± 10.6	7.25	2.92	4.4 ± 4.4	0.75	0.27	—	—	—
Punctum pygmaeum	35.4 ± 14.1	12.64	3.27	13.3 ± 7.4	4.55	1.15	8.8 ± 6.2	1.59	0.13
Discus rotundatus	30.9 ± 11.5	243.10	62.01	26.5 ± 14.9	322.97	81.86	8.8 ± 6.2	42.48	11.32
Hygromia striolata	17.7 ± 8.0	667.46	359.83	—	—	—	4.4 ± 4.4	9.06	1.64
Arianta arbustorum	4.4 ± 4.4	1,502.80	813.28	—	—	—	—	—	—
Total	1,082 ± 145.0	2,887.97	1,380.50	185.0 ± 38.9	482.10	155.99	472.8 ± 91.9	322.84	96.19

of sub-samples. The autumn population of *Punctum pygmaeum* was significantly higher than the preceding spring population, but fell again by the following spring.

Carychium tridentatum populations were highly aggregated on each sampling occasion. Using the test of David and Moore (1954) the aggregation on 29th June 1968 was shown to be significantly higher than that of the preceding and following sampling occasions. The other four species showed aggregation at certain times of the year only.

The validity of using a single sampling occasion to obtain a population index for other sites is dealt with in the Discussion. Table 4 gives the results of sampling the subsidiary Sites 2—4. Site 2 had a significantly higher population density and biomass than Site 1, *Carychium tridentatum* being more numerous and *Arianta arbustorum* markedly increasing the biomass. Site 3 had a lower population density and biomass than Site 1. *Cochlicopa lubrica* was of increased importance on Site 4.

Production of Litter

Table 6 shows the monthly input of tree litter. The input of material other than beech was small, consisting chiefly of leaves and fruits of hornbeam and leaves of chestnut. Much smaller amounts of sycamore, oak, birch and privet litter were collected. That litter which was not beech is combined into "other litter" in Table 6. The seasonal production of beech litter components as a percentage of their annual production is given in Table 7. A total production of 652.4 ± 58.8 g/m²/annum was recorded, of which 584.4 g/m²/annum were of beech material. 72% of the total beech litter production fell in the October-December period. Leaves (337.9 g/m²/annum) made up 58% of the total beech litter fall. Bud scales and flowers (30.1 g/m²/annum) made up 5.2% of the total litter fall, while fruits (consisting of cupules and seeds), at 157.7 g/m²/annum, made up 27% of the total. Fruits falling in winter and spring consisted chiefly of empty cupules; summer fall was of unripe fruit. 10% of the total litter fall (58.7 g/m²/annum) consisted of twigs and bark. 42% of the total litter fall consisted of non-leaf material.

The standing crops of the field layer species are given in Table 8. The maximum potential field layer litter input was calculated as the sum of the maximum standing crops of the individual species, and was 23.3 g/m². The total litter production (tree and field layer litter) was therefore 675.7 g/m²/annum, of which 3.4% was contributed by the field layer.

The litter standing crop on 17th September 1968 is given in Table 9, and amounted to a total of 2,700 g/m².

Table 6. *The monthly input (mean + SE) of litter in a beech stand (Site 1) in Wytham Woods, Berkshire, 1968—69 (g/m²)*

Month	Beech litter				Other litter	Detritus	Total
	leaves	bud scales	fruits	twigs and bark			
July	3.50 ± 0.40	0.81 ± 0.10	1.83 ± 0.04	4.48 ± 1.48	1.27 ± 0.46	3.50 ± 0.30	15.4 ± 2.0
August	9.26 ± 0.61	0.31 ± 0.12	5.09 ± 0.87	3.10 ± 0.61	2.28 ± 0.82	2.75 ± 0.36	22.7 ± 1.2
September	29.27 ± 3.05	0.05 ± 0.05	14.25 ± 1.99	20.51 ± 6.26	5.33 ± 1.82	1.42 ± 0.32	70.2 ± 10.0
October	129.18 ± 32.58	0.03 ± 0.03	71.62 ± 7.00	3.21 ± 1.42	11.94 ± 4.64	2.19 ± 0.47	218.7 ± 32.7
November	152.20 ± 4.50	—	36.40 ± 5.10	2.55 ± 0.81	22.43 ± 6.26	1.22 ± 0.15	217.9 ± 7.2
December	8.19 ± 2.72	—	12.52 ± 1.78	5.40 ± 1.43	4.39 ± 1.24	1.07 ± 0.19	31.4 ± 2.9
January	0.53 ± 0.15	—	4.96 ± 1.35	2.97 ± 2.06	0.92 ± 0.31	0.61 ± 0.22	10.0 ± 2.3
February	0.41 ± 0.16	—	1.02 ± 0.32	6.49 ± 3.37	0.16 ± 0.09	0.66 ± 0.14	8.7 ± 3.5
March	0.59 ± 0.20	0.08 ± 0.15	1.22 ± 0.39	0.51 ± 0.12	0.18 ± 0.06	0.23 ± 0.08	2.8 ± 0.5
April	0.76 ± 0.07	0.66 ± 0.15	2.90 ± 0.76	1.32 ± 0.41	0.07 ± 0.07	0.92 ± 0.31	6.4 ± 0.8
May	1.43 ± 0.16	25.85 ± 1.17	3.36 ± 1.07	4.89 ± 1.53	—	1.07 ± 0.20	36.6 ± 2.6
June	2.55 ± 0.30	2.34 ± 0.30	2.55 ± 0.60	3.26 ± 1.05	—	1.02 ± 0.15	11.6 ± 1.6
Total	337.87 ± 34.43	30.13 ± 1.54	157.72 ± 22.11	58.69 ± 20.05	48.97 ± 15.71	16.66 ± 2.32	652.4 ± 58.8

Table 7. *The seasonal production of beech litter components as a percentage of their annual production (data taken from Table 6)*

Season	Total	Beech leaves	Bud scales and flowers	Fruits	Twigs and bark
July to September	15.8	12.4	4.0	13.4	47.7
October to December	72.1	85.7	—	76.4	19.0
January to March	3.2	0.4	—	4.6	17.0
April to June	8.9	1.4	96.0	5.6	16.1

Table 8. *The field layer standing crop (g/m²) beneath beech trees in Site 1, sampled in April and July 1969*

Species	17. 4. 69 field layer standing crop (g/m²)	20. 7. 69 field layer standing crop (g/m²)
Mercurialis perennis	2.14 ± 0.54	14.88 ± 4.40
Circaea lutetiana	—	3.28 ± 0.73
Viola reichenbachiana	0.24 ± 0.10	—
Crataegus monogyna	0.13 ± 0.11	0.31 ± 0.22
Ligustrum vulgare	0.27 ± 0.12	1.29 ± 0.82
Geranium robertianum	0.06 ± 0.05	—
Galium aparine	0.02 ± 0.02	—
Geum urbanum	0.08 ± 0.07	0.12 ± 0.12
Urtica dioica	—	0.98 ± 0.98
Rubus fruticosus	—	0.52 ± 0.52
Holcus mollis	0.04 ± 0.04	—
Acer pseudoplatanus	0.71 ± 0.09	1.00 ± 0.24
Fagus sylvatica	—	0.09 ± 0.09
Fraxinus excelsior	—	0.46 ± 0.28
Total	3.49 ± 0.62	21.20 ± 4.62

Table 9. *The litter standing crop on the woodland floor of Site 1 on 17th September 1968*

Litter type	Dry wt. in g/m²
Branches + twigs (> 1 cm diam.)	675
Twigs (< 1 cm diam.)	340
Fruits	478
Leaves	1,306
Total	2,700 ± 250

Consumption of Food by Snails

Mason (1970) showed that litter forms the chief dietary component of woodland snails. Mean daily ingestion was 0.93% of dry body weight and 2.83% of ash-free dry body weight of snails at 10°C (see Discussion). These values were used to calculate the annual ingestion of litter by populations of snail species on Site 1 at a mean annual field temperature which was close to that used for laboratory determined feeding rates;

Table 10. *Estimated annual ingestion by the mollusc populations at Site 1*

Species	Annual ingestion (mg)	
	calculated from dry wt. of animal	calculated from ash-free dry wt. of animal
Carychium tridentatum	223.49	137.50
Cochlicopa lubrica	10.55	11.86
Columella edentula	6.39	9.71
Pupilla muscorum	0.73	0.73
Vallonia pulchella	3.07	2.59
Acanthinula aculeata	172.65	232.21
Ena obscura	179.76	242.21
Marpessa laminata	31.65	27.89
Clausilia bidentata	18.69	14.67
Vitrea contracta	74.90	96.69
Retinella radiatula	2.92	3.72
Retinella pura	73.40	104.83
Retinella nitidula	92.53	132.13
Oxychilus alliarius/cellarius	543.85	718.43
Euconulus fulvus	6.86	8.98
Punctum pygmaeum	65.81	43.07
Discus rotundatus	303.72	240.90
Vitrina pellucida	7.26	14.89
Hygromia striolata	555.53	826.76
Hygromia hispida	4.71	2.59
Total	2,372.46	2,872.33

the results are given in Table 10. Using the value of 0.93% the ingestion of food by the total snail population was calculated as 2,372.43 mg/m²/annum, and 2,872.33 mg/m²/annum using the value of 2.83%. As the annual litter input was 675.7 g/m²/annum, the snail population ingested only 0.35—0.43%. The mean percentage assimilation of litter by snails was 49.1% (Mason, 1970), thus snails on Site 1 assimilated only 0.17—0.21% of the annual litter input.

Discussion

Populations of Snails

Various sampling techniques have been used for extracting snails from litter and soil, none of them wholly successful. Direct collections from the field, using quadrats or transects, were made by Foster (1937), Strandine (1941), Goodhart (1962), Owen (1965), Berry (1966), Baker (1968), Grime and Blythe (1969) and Pomeroy (1969). The method is only suitable for large and conspicuous species; young individuals and concealed animals are probably under-represented in the samples. Sieving methods were used by Økland (1929) and Jacot (1935), but their methods do not adequately distinguish between live and dead animals, whereas the technique of Williamson (1959) does; however, this method is not absolutely quantitative. Vágvölgyi's (1952) flotation method, subsequently used by Agócsy (1968) is quantitative and does distinguish between living and dead animals; in these two instances, however, the extraction efficiency was not determined. A modification of Vágvölgyi's (1952) method was used in the present study. Narcotisation of living animals, to ensure that they did not attach to leaves etc., was avoided; it was found simpler to kill them by putting samples into hot water and stirring vigorously to detach them. Most litter, with the dead shells, floated on the water surface and could be discarded. Little litter remained on the water surface in the second float, insufficient to justify the use of potassium hydroxide as a wetting and macerating agent. Handling of samples was thus simplified. The extraction efficiency was 84%, falling well within the 95% confidence limits of the population estimates.

On Site 1 the mean population density was 489 snails/m^2. Within the sampling programme adopted, the monthly fluctuations in four of the five common species were not shown to be significantly different, but in the fifth species, *Punctum pygmaeum*, the autumn population was higher than that in spring. This apparent general stability of the snail population is a somewhat unusual situation in invertebrates. Woodland molluscs tend to have extended breeding seasons, often over most of the year (Taylor, 1894—1914; Frömming, 1954) though there may be a peak in breeding activity. The number of eggs laid is comparatively small, normally less than fifty, whilst the life-span of snails is of the order of $1^1/_2$—3 years (Taylor, 1894—1914; Frömming, 1954) e.g. about $2^1/_2$ years in *Carychium tridentatum* (Morton, 1954). Thus, with a long breeding season producing few offspring, and a long lifespan, changes in natality and mortality over a year are probably not sufficiently large to be detected by the present sampling regime. It is

suggested that sampling only once or twice a year may be adequate to obtain an acceptable measure of density in such constant populations.

Soil and litter animals are normally aggregated (Debauche, 1962) and examples are known from molluscs (South, 1965; Hunter, 1966; Baker, 1968; Pomeroy, 1969). A variety of indices have been devised for determining the degree of aggregation, though all are dependent on sample size (Grieg-Smith, 1964). The variance: mean ratio was used in the present instance, and as the number and size of samples was constant for all species, the indices of aggregation can be compared. *Carychium tridentatum* was most aggregated; the index increased markedly in late June, possibly the period of peak breeding (June was the principle month of egg-laying in a population studied by Morton, 1954). Aggregation was less pronounced in other species, occurring in April and July with *Acanthinula aculeata*, June, January and February with *Punctum pygmaeum*, May, June and October with *Vitrea contracta* and June with *Retinella pura*. There is no information in the literature on the peak breeding times of these species and it is not possible to comment on the effect of their breeding activity in relation to aggregations. Other factors, such as humidity and temperature, may affect aggregation. Thus Lloyd (1963) observed many invertebrates, including snails, moving from logs to litter during cold weather, and hence changing their pattern of dispersion. The aggregations themselves accounted for much of the spread of the confidence limits.

It was suggested above that one sampling period per year may be sufficient to obtain a good index of population density in various sites. This method was used on the subsidiary Sites 2—4. The snail population on Site 2 was much higher than that on Site 1, while Site 3 had a lower population. All three sites consisted of beech stands of equal age in fairly close proximity. Site 2 had, however, a dense field layer and was less exposed than Site 1, while Site 3 had a sparse field layer and was more exposed. *Carychium tridentatum* was the dominant species in all three beech sites, and in the oak-ash-sycamore stand (Site 4). There is obviously much variation in population densities in individual sites, due probably to differences in substrate, pH, soil moisture and vegetation (Agócsy, 1968; Valovirta, 1968; Wäreborn, 1969).

Few comparative data on population densities of terrestrial snails exist; the use of different sampling and/or extraction techniques, many of them inadequate, complicates the comparison. Økland (1929), using a sieving method, found a density of 250 snails/m^2 in Norwegian woodlands. Mörzer-Bruijns *et al.* (1959) had average abundances of 100—400 snails/m^2 in oak and beech woodlands in the Netherlands. In Hungarian oakwoods Agócsy (1968), using Vágvölgyi's extraction method,

had mean densities of 320 snails/m² on limestone and 28 snails/m² on sandstone substrates. Valovirta (1968), using Økland's (1929) sieving technique, recorded densities of 123—225 snails/litre of litter in Finnish woodlands. Although the results from different woodlands are not strictly comparable it should be noted that the population densities recorded in the present study are slightly higher, possibly due to a more efficient extraction technique.

Higher population densities are reached in specialised habitats. For instance, Berry (1966), hand-sorting samples from exposed Malayan limestone cliffs, found populations of 3,197/m² on mossy rocks and 1,579/m² on moss-free rocks.

Population densities of single species have been determined by Foster (1937), Strandine (1941), Goodhart (1962), Owen (1965), Baker (1968), Grime and Blythe (1969) and Pomeroy (1969). Population densities in relatively open grassland or shrubland sites generally ranged from 1—20 snails/m², but *Helicella caperata* on English sand-dunes peaked at 232/m² (Baker, 1968), while *Helicella virgata* in south Australian shrublands had a mean density of 158/m² (Pomeroy, 1969); both populations showed considerable seasonal variation. The highest single species density in the present study was of 751 *Carychium tridentatum*/m² on Site 2 and the lowest was 0.07 *Pupilla muscorum*/m² on Site 1.

The biomass standing crop of snails has been determined in only a few studies. The biomasses of snails in Danish forests (4—146 mg live wt./m²) determined by Bornebusch (1940) are considered extremely low and probably due to inadequate sampling techniques (Birch and Clark, 1953). 15.8 g of *Polygyra thyroides* protoplasm/m² from Illinois floodplains and 339 mg *Succinea ovalis* protoplasm/m² from Illinois forests were recorded by Foster (1937) and Strandine (1941) respectively; assuming protoplasm to be approx. 75% water, the dry weight is 4 g/m² for *Polygyra* and 84 mg/m² for *Succinea*, the former markedly higher than the total snail biomass standing crop/m² at the Wytham sites. Pomeroy (1969) determined an average biomass of 15—20 g live wt./m² of *Helicella virgata* in shrubland in south Australia; this is approx. 6.3—8.4 g dry wt./m² or 1.6—2.2 g ash-free dry wt./m² (personal observations), considerably higher than the total population biomass/m² in Wytham. Using personal data on the biomass of *Cepaea nemoralis* and *Arianta arbustorum*, a biomass of 4 g dry wt./m² and 3 g dry wt./m² for *Cepaea* and 7.5 g dry wt./m² for *Arianta* in grasslands can be calculated from the population densities given by Goodhart (1962) and Grime and Blythe (1969), though these are probably overestimates as they are based on biomasses of adult animals.

From the limited data available it is tentatively suggested that the greatest population densities, and species diversity, of snails occurs in woodland habitats; however greatest biomasses, of a few large species, occur in more open habitat, e.g. grasslands.

Litter Production

Much work has been done on beech litter production on the European continent, beginning with the classic studies of Ebermayer (1876) and Danckelmann (1887), who studied litter production in relation to tree age, as did Möller *et al.* (1954b) and Bonnevie-Svendsen and Gjems (1957). Beech litter production on soils of different quality was studied by Danckelmann (1887), Járó (1958) and Zangiyev (1960). Möller *et al.* (1954b), Bonnevie-Svendsen and Gjems (1957), Zangiyev (1960), Donov (1964) and Myczkowski (1967) divided beech litter input into its various components. Litter production in general has been excellently reviewed by Bray and Gorham (1964).

Site 1 in Wytham Wood had an annual beech litter production of 584.4 g/m^2, which is very high when compared with the mean litter fall of 28 sites (including the present) in Europe, 360 g/m^2/annum. In addition to the present study, relatively high deciduous litter falls recorded from cool temperate forests are those of Sviridova (1960), who reported 600 g/m^2/annum in a stand of *Populus* sp. and Megalinski and Orlov (1965), who calculated 580 g/m^2/annum in a 25—30 years old stand of sycamore.

Fifty-eight per cent (337.9 g/m^2/annum) of the beech litter fall in the present study consisted of leaves and 83% of this fell in October-November. Bonnevie-Svendsen and Gjems (1957) in Norway found that 71—92% (157.2—286.2 g/m^2/annum) of the beech litter fall was accounted for by leaves, similarly 75% (290.5 g/m^2/annum) of Myczkowski's (1967) annual beech litter fall in Poland was leaves. The mean leaf litter production of twelve studies (including the present) was 260 g/m^2/annum. The percentage of leaves in the present study was low, probably due to the high fruit production in that year. Kira and Shidei (1967) point out that the ratio of non-leaf components to leaves in litter is greater than $^1/_2$ in all cases studied and sometimes approaches $^1/_1$ in some climax forests.

Of the bud-scales and flowers, 85.5% (25.9 g/m^2) fell in May. Myczkowski (1967) recorded 6.3 g/m^2/annum of bud-scales and flowers, amounting to 1.6% of total litter fall (cf. 30.1 g/m^2/annum, 5.2% of the total litter fall, in the present study).

The fruit fall in the present study amounted to 27.0% (157.7 g/m^2/annum) of the total litter fall. Donov (1964), collecting litter from 19th September to 28th November, recorded a fruit fall of 20 g/m^2, this being

0.8% of the total litter fall in the period. Myczkowski (1967) had a seed production of 4.4 g/m²/annum (1.1%). The figures in the present study indicated a good fruiting season.

Twigs and bark (58.7 g/m²/annum) made up 10% of the total litter fall in the present study. 35% of the fall occurred in September, due to the effect of gales on heavily laden trees. Twig and bark fall was fairly constant over the rest of the year. Donov (1964) had a loss of 7 g/m² from 19th September to 28th November, being 2.8% of the total litter production during the period, and agreeing closely with 2.7% of the total litter loss in the October-December period in the present study. Myczkowski (1967) had a twig and bark litter of 74.7 g/m²/annum, 19.4% of the total litter loss. Möller *et al.* (1954a) recorded an annual branch and twig loss of 1,200 g/m² in a 50 years old beech stand, their study being continued over six years and hence taking into account the erratic loss of larger branches.

The large litter fall in the present study was due to high production of leaves, bud-scales and fruits; fruit production is notoriously variable and would presumably not form such a high proportion of litter-fall in all years. The high production may be due to a combination of good soil conditions, mild and wet climate, and the age of the trees, but it is unwise to generalise on one year's data.

The above-ground field-layer crop was taken as a measure of the potential litter-production. It was approximate and assumed that premature leaf senility and die-back had not occurred prior to sampling, and that no further growth occurred in the field after sampling. The above-ground field layer standing crop (23.29 g/m²) amounted to only 3.4% of the total litter input. Comparative figures are those of Ovington (1955), who recorded 16.2 g/m² in a young beech plantation in western England. Kazmierczakow (1967) had a peak above-ground field-layer standing crop in June of 4.4 g/m² in a Polish beech forest.

If the value for the annual litter fall is divided into the total litter standing crop, a crude measure of the litter turnover time is obtained. The mean turnover time of the litter was calculated as 4.6 years. Myczkowski (1967) calculated that a period of at least 3 years was necessary for the total decomposition of beech litter in Poland. In the present study the approximate turnover time of leaves was 4.0 years, of twigs 6.0 years and of fruits 3.0 years (though the probable high fruit production in autumn 1968, plus the removal of seeds by rodents and birds, has probably resulted in a considerable over-estimate). Bonnevie-Svendsen and Gjems (1957) considered their estimates of 3.2 and 1.6 years for beech leaf decomposition to be minimal. There was a 35% decrease in weight of beech leaves in litter bags at 900 m in Japan after the first year (Kira and Shidei, 1967).

The Role of Snails in Litter Decomposition

Mason (1970) showed that woodland snails feed primarily on dead plant material, though living plant material, fungi and dead animal remains also occur in small amounts, and to different extents, in different species. In the present study the laboratory ingestion and assimilation rates of snails feeding on leaf litter at 10°C (from Mason, 1970) have been used to calculate the annual ingestion in field populations, this being considered the best approximation. The mean annual litter temperature on Site 1, determined by using the sucrose inversion method of Berthet (1960), was 8°C (unpublished observations); the field ingestion per annum calculated at 10°C will therefore be slightly overestimated. Ingestion rate per g live wt. snail and percentage assimilation for large species (*Helix aspersa, Hygromia striolata, Oxychilus cellarius*) did not differ from that of smaller species (*Discus rotundatus*); a mean value for ingestion rate was therefore used to calculate the annual ingestion of all species occurring in the population.

The snails on Site 1 ingested only 0.35—0.43% of the annual litter input, suggesting that they are of little importance in litter decomposition. The literature contains little information on the role of invertebrate decomposer groups. Drift and Witkamp (1958) calculated that the terrestrial caddis *Enoicyla pusilla* removed approx. 9% of the annual litter input in a Dutch oak-wood. Diplopods and Isopods ate 3—4% of the leaf litter in a Hungarian *Querceto-Potentilletum albae* forest (Gere, 1963). Adult Oribatids utilised approx. 1.8% of the leaf litter input in a Belgian forest (Berthet, 1963); the total population removed about 20% (Berthet, 1967). The millipede *Glomeris marginata* consumed 1.7—10% of the annual litter fall in an English woodland (Bocock, 1963). It seems probable that micro-organisms are responsible for 80—90% of the metabolism in decomposer systems (Macfadyen, 1961, 1963); thus the role of animals in litter decomposition will appear small. Their chief importance is probably in physically and chemically altering the litter, and hence promoting fungal and microbial growth. According to Edwards and Heath (1963), they are essential in these early stages of litter breakdown. The low assimilation of most litter feeders, and hence their high faeces production, facilitate the process. Although snails are primarily plant litter feeders, they nevertheless can eat a wide variety of foods, and probably do when they become available (e.g. *Oxychilus cellarius* in Wytham Woods was attracted in large numbers to scattered grain). Darnell (1968) considered such nutritionally flexible species to be the primary day-to-day regulators of the community, hence the role of snails may be more important than their litter consumption suggests.

Slugs were not examined in the present study, different techniques for sampling and extraction being required. They may, however, be of

some importance in decomposition processes. Bornebusch (1930) determined the biomass of slugs and snails on five beech woodland sites in Denmark. The biomass ratio of slugs: snails had the range 10—51 (mean 38). Using the mean ratio of 38:1, and assuming that the consumption rate per unit live weight of slugs, and their diet, is the same as that of snails, they could remove as much as 16% of the annual litter production on Site 1, of which about 8% would be assimilated. However, it must be remembered that Bornebusch's sampling techniques were inadequate, and therefore the ratio used above may be incorrect. A precise evaluation of the role of slugs in woodland ecosystems would be most valuable.

It is considered impracticable to determine, at one and the same time, the roles of every species living within a community and the concept of the key species is frequently adopted. Key species are animals that subjectively appear to be important in ecosystems i.e. usually those that are the largest or most numerous. Key species may provide a rapid evaluation of the functioning of the ecosystem. The data in Table 10 are used to examine the validity of the key species concept. The sum of the annual ingestion of the three most numerous species (*Carychium tridentatum, Punctum pygmaeum* and *Acanthinula aculeata*) was 9.5 or 14.5% of the total annual ingestion by snails (depending whether the dry weight or ash-free dry weight biomasses are used for computation). The sum of the annual ingestion of the four largest species (*Oxychilus cellarius/alliarius, Hygromia striolata* and *Marpessa laminata*) is 47.7 or 54.8% of the total ingestion by snails. Thus the importance of the scarce species, when summed, is far greater than that of the abundant species, and the effect of small animals, when summed, is as important as the large species. A similar analysis was made by Berthet (1967) for the metabolic activity of species populations of Oribatid mites. In the sites studied, four species usually accounted for 50% of the metabolic activity, these dominant species usually being of larger size, though in some communities smaller species, because of higher population density, were also individually important. In complex systems, with a high species diversity, the key species concept must be used with caution.

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