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Population structure, density, dispersal and neighbourhood size in *Arianta arbustorum* (LINNAEUS, 1758) (Pulmonata: Helicidae)

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(With 3 Figures)

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Summary

Field studies on the ecology of the land snail *Arianta arbustorum* (LINNAEUS, 1758) in the Alps and Scandinavia are reviewed. Emphasis has been given to the spatial distribution of individuals, population structure, population density and dispersal. Estimates of neighbourhood size are presented for continuously distributed populations of *A. arbustorum*.

Zusammenfassung

Die vorliegende Arbeit faßt die Literatur über die räumliche Verteilung von Individuen und Populationen, die Populationsdichte und Ausbreitungsleistung der Landschnecke *Arianta arbustorum* (LINNAEUS, 1758) in den Alpen und Skandinavien zusammen.

Populationen von *A. arbustorum* können verschiedene räumliche Strukturen haben. Berghänge können flächendeckend von Schnecken besiedelt sein. Wegen ihrer limitierten Vagilität sind Individuen, die mehr als 50 m voneinander entfernt aus Eiern geschlüpft sind, voneinander isoliert, da diese Distanz größer ist als die totale Ausbreitungsleistung beider Tiere (isolation-by-distance model). Aus der Perspektive der Populationsgenetik bedeutet dies, daß eine große, flächendeckende Population aus mehreren, aneinandergrenzenden Teilpopulationen aufgebaut ist. Die Größe dieser Teilpopulationen hängt von der lokalen Dichte (Anzahl Individuen pro m^2) sowie von der Ausbreitungsleistung der Schnecken ab. Bei *A. arbustorum* wurden 'neighbourhood sizes' von 388 bis 5600 Individuen geschätzt. Die 'neighbourhood area' entspricht einer kreisrunden Fläche von 32 bis 50 m Durchmesser. *A. arbustorum* kann aber auch in isolierten Populationen in geeigneten Habitatpatches auf klar abgrenzbaren Flächen vorkommen. Sind solche Populationen durch lineare Habitatstrukturen wie Bachufer, Rinnenböschungen oder Wegränder, welche einen Austausch von Schnecken ermöglichen, miteinander verbunden, spricht man von einer Metapopulation.

Innerhalb einer Population kommt *A. arbustorum* häufig aggregiert vor. Die kleinräumige Verteilung von *A. arbustorum* variiert mit der Heterogenität des Habitates und den vorherrschenden Wetterbedingungen; bei trockenen Bedingungen sind die Tiere am intensivsten aggregiert.

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Die Populationsdichte von *A. arbustorum* variiert von 0,1 bis 20 adulte Tiere/m² in verschiedenen Habitaten. Die Dichte scheint von verschiedenen Faktoren beeinflußt zu sein, und so kann einem bestimmten Habitattyp keine charakteristische Dichte zugeordnet werden.

In drei alpinen Populationen wurde festgestellt, daß adulte Schnecken sich im Durchschnitt 7–12 m pro Jahr von ihrem Ausgangspunkt entfernen. Dabei bewegen sich die Tiere hauptsächlich entlang von Rinnen und Bächen. Die Länge der täglichen Dislokationen von adulten *A. arbustorum* variiert zwischen 0 und 4,44 m (Median 0,58 m); sie ist vom Habitattyp, den vorherrschenden Wetterbedingungen, sowie von der Jahreszeit abhängig. Passive Verfrachtungen von Individuen durch Lawinen und Hochwasser und Hinunterkollern über steile Hänge, Felswände und Schneefelder dürften eine wichtige Rolle für die Ausbreitung der Art und für den Genfluß zwischen bestehenden Populationen bilden. Durch aktives Aufwärtskriechen (negative geotaktische Reaktion) können die Schnecken die talwärts gerichteten Verfrachtungen kompensieren.

Acknowledgement

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1. Introduction

Helicid snails are suitable organisms for research in evolutionary biology. They are easy to collect and to mark, are common in a variety of habitats, and are often highly polymorphic (CAIN 1983). *Cepaea nemoralis* (LINNAEUS, 1758) has been extensively studied (for reviews see JONES, LEITH & RAWLINGS 1977; CLARKE, ARTHUR, HORSLEY & PARKIN 1978), but other species including *Arianta arbustorum* (LINNAEUS, 1758) have also attracted attention. The great variability of shell size, colour and shape, as well as a wide altitudinal distribution (i.e. differential selection pressures within short geographical distances), make *A. arbustorum* a particularly suitable candidate for taxonomic and evolutionary questions (e.g. COOK 1965; COOK & KING 1966; BURLA & STAHEL 1983; BURLA 1984; BAUR 1986a; NEMESCHKAL & KOTHBAUER 1988, 1989; ARTER 1990; NEMESCHKAL 1990, 1991; GITTENBERGER 1991; KOTHBAUER, NEMESCHKAL, SATTMANN & WAWRA 1991; B. BAUR & A. BAUR 1992).

The spatial pattern of genetic diversity in a species is largely determined by the effects of three fundamental evolutionary forces: natural selection, genetic drift, and gene flow (e.g. SLATKIN 1985, 1987). Knowledge of population structure is essential for understanding evolutionary processes. For a discrete, panmictic population, the effective population size is the size of an idealized population equivalent genetically to a real one. This concept is not applicable to a continuously distributed population where the neighbourhood size, combining both density and dispersal within the population, is appropriate. Most real populations will probably be intermediate in structure between the discrete and continuous models. Furthermore, both density and dispersal have considerable ecological interest in their own right.

The purpose of this review is to bring together diverse information on population structure, density, dispersal and neighbourhood size in *A. arbustorum*.

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Other aspects of the ecology and behaviour of *A. arbustorum* have been studied. Information is available on life-history (TERHIVUO 1978; ANDREASSEN 1981; BAUR 1984a, b, 1988, 1990; RABOUD 1986; BAUR & RABOUD 1988), predation and competition (REICHARDT, RABOUD, BURLA & BAUR 1985), and egg cannibalism (BAUR 1992). These aspects are discussed when relevant; no attempt is made, however, to cover the extensive studies on shell variation, for which BURLA & STAHEL (1983) and NEMESCHKAL & KOTHBAUER (1988, 1989) provide many references.

2. Spatial distribution of individuals and populations

2.1 Microdistribution

The distribution exhibited by a group of organisms depends on the spatial scale on which the organisms are studied. The problems of measuring and interpreting spatial distributions are discussed by SOUTHWOOD (1978) and GREIG-SMITH (1983). An examination of microdistribution is an important preliminary to many kinds of field investigation, including habitat selection, density estimates, and dispersal studies.

Within a population, *A. arbustorum* is often aggregated (or clumped) (ANDREASSEN 1981; BAUR 1984c, 1986b). Aggregations are most pronounced at a patch size of 25 cm × 25 cm; this area corresponds approximately to that covered by a herb or grass tuft in an alpine meadow (BAUR 1984c, 1986b). The intensity of aggregation varies with season, being highest under dry conditions in summer. An aggregated dispersion pattern at a small scale can be the result of habitat heterogeneity (such as a heterogeneous stone or vegetation cover) or social attraction. Furthermore, the snails' preference for a particular plant species (either as food resource or resting site) can result in an aggregated distribution. *Arianta arbustorum* frequently feeds on nettles (*Urtica dioica*) and thistles (*Cirsium arvense)*, whereas aconite (*Aconitum compactum*) serves as resting site in alpine pastures (FRÖMMING 1954, BAUR 1984c, 1986b). On aconite the snails are protected against trampling and accidental predation by cattle (alkaloids make aconite unpalatable for cattle). However, there is no experimental evidence for an active choice of aconite by *A. arbustorum* to avoid predation and trampling.

In general, aggregations of *A. arbustorum* are most pronounced in highly heterogeneous habitats (e.g. scree-covered mountain slopes) and under harsh environmental conditions (e.g. drought).

2.2 Spatial distribution of populations

The spatial distribution of populations (or demes) of *A. arbustorum* is influenced by the heterogeneity of the landscape. Depending on ecological conditions (e.g. moisture of the microhabitat, calcium content of the soil, type and height of the vegetation, availability of food plants, oviposition sites and resting sites), *A. arbustorum* occurs in band-like (linear) or two-dimensional assemblages of different size. On mountain slopes, *A. arbustorum* can be continuously

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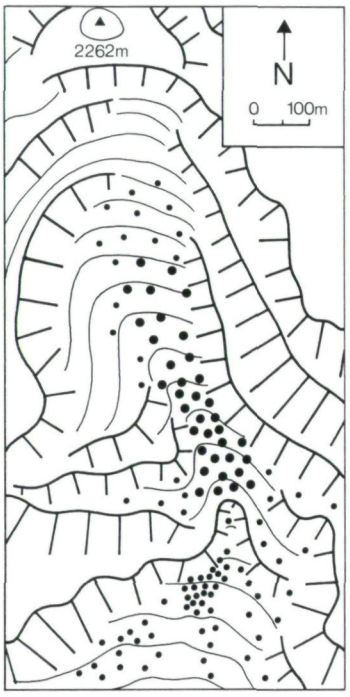

Fig. 1: Spatial distribution of *A. arbustorum* at Valsloch (south slope of the Chäserrugg, Churfirsten mountains, eastern Switzerland, 1750–2150 m a.s.l.) in August 1982. Large points indicate 10000 snails, small ones 1000 snails. Contour interval 20 m.

distributed over large areas (Fig. 1), reaching a total of several million individuals. In contrast, isolated populations consisting of a few hundred or less individuals can exist in small patches of marginal habitat (Fig. 2). At Hinter-Öhrligrueb (Alpstein mountains, eastern Switzerland), *A. arbustorum* inhabits the patch (40 m × 80 m in size) which is first free of snow in spring.

At Potersalp (Alpstein mountains, eastern Switzerland), *A. arbustorum* was found in pastures along ditches and streams (almost linear populations), and in marshes (two-dimensional populations), while it was absent in bogs and in the forest, where the soil is acidic (Fig. 3). In some parts of the stream banks no *A. arbustorum* could be found with repeated checks. In these small valleys, snow remained until the beginning of July in 1982, while the surroundings had been free of snow for 40 days. This mosaic of occupied and unoccupied habitat patches can be best described by a metapopulation concept (for a review see HANSKI & GILPIN 1991). Figure 3 illustrates such a system of local populations connected by dispersing individuals.

In the absence of environmental changes, the spatial distribution of *A. arbustorum* populations appears to be rather stable in time. The surveys presented in Figs 2 and 3 were repeated 11 and 10 years later. At Hinter-Öhrligrueb (Fig. 2), the soil of the western part of the isolated patch suitable for *A. arbustorum* had

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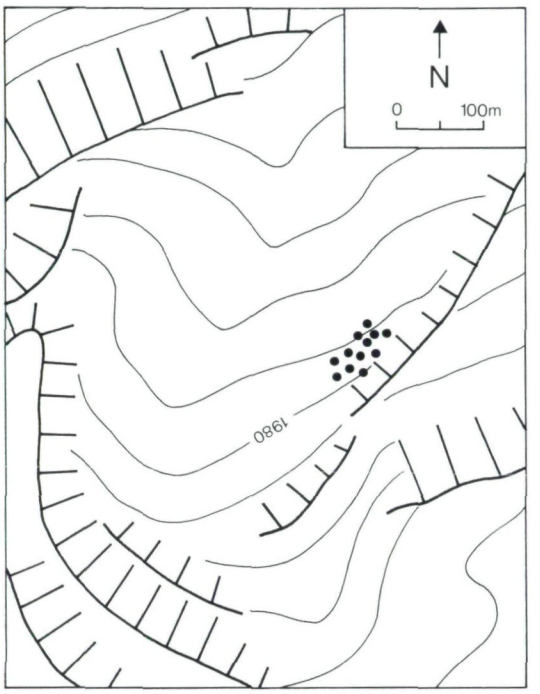

Fig. 2: Isolated population of *A. arbustorum* at Hinter-Öhrligrueb (Alpstein mountains, eastern Switzerland, 1980 m a.s.l.) in August 1981. Points indicate 20 snails. Contour interval 20 m.

been eroded between the two surveys, but snails still occurred in the remaining part in 1992, although in a significantly lower number. At Potersalp (Fig. 3), the mosaic-like structure of *A. arbustorum* populations in 1991 was very similar to that monitored 10 years previously, although changes in abundance were observed.

Natural habitats are increasingly changed and destroyed by human activities. A field survey revealed that *A. arbustorum* went extinct at 16 (55.2%) of 29 localities in the surroundings of Basel (Switzerland) between 1908 and 1991 (B. BAUR & A. BAUR 1993). Habitat destruction by urban development was the reason for extinction of eight local snail populations. There is some evidence that local climatic warming due to thermal radiation from urban areas might have caused the extinction of eight further populations, for eggs of *A. arbustorum* do not develop when the temperature exceeds 24°C at the oviposition site (B. BAUR & A. BAUR 1993).

3. Density

Density estimates of *A. arbustorum* have usually been made either by direct counting of snails within quadrats or by applying mark-release-recapture techniques. Direct counting is liable to underestimate small snails. ANDREASSEN (1981) developed a correction factor to compensate for the easily overlooked

Table 1: Summary of population density estimates in *A. arbustorum*

Habitat, Vegetation	Country	Density (No. ind./m²)	Size class	Time of year	Method	Source, Remarks
N-exposed mountain slope, *Mercurialis perennis*	GB	9.7	> 10 mm	August	QS[1])	GRIME & BLYTHE (1969)
Beech forest, *Mercurialis perennis*	GB	4.4	all snails	June	QS[1])	MASON (1970)
Riparian forest	Germany	46	all snails	February-May	QS[1])	REICHHOLF (1979)
Slope, grassland with *Filipendula ulmaria*	Norway	0.6–6.8	adults	2 years, at intervals of 3 wk	QS[1])	ANDREASSEN (1981)
Stands of nettle (*Urtica dioica*) and *Filipendula ulmaria*	Norway	11.3 and 17.3	adults	June	MRR[2])	ANDREASSEN (1981) (2 populations)
Subalpine pasture, along a ditch	Switz.	20.0	> 8 mm	August	MRR[2])	BAUR(1986b)
Subalpine pasture, embankment of a stream	Switz.	3.9	adults	September	MRR[2])	BAUR(1986b)
Scree-covered mountain slope with few grass tufts	Switz.	0.1	adults	August	MRR[2])	BAUR (1986b)
Belt of nettle *Urtica dioica* and *Aconitum compactum*	Switz.	5.9	adults	September	MRR[2])	BAUR (1986b)
Alpine grassland with scree material	Switz.	2.4	adults	August	MRR[2])	BAUR (1986b)
Uncultivated meadow with *Rubus corylifolius*	Switz.	42.2	> 8 mm	September	MRR[2])	BAUR (1986b)
Marshy pasture	Switz.	2.2	adults	July	QS[1])	BAUR (1986b)
Alpine grassland with little scree material	Switz.	5.0	adults	August	QS[1])	BAUR (1986b)
Clearings with grass and *Cirsium arvense*	Sweden	4.3–10.8	adults	August	MRR[2])	BAUR (1988) (range of 9 populations)
Stands of aspen (*Populus tremula*) and ash (*Fraxinus excelsior*)	Sweden	1.9 and 6.3	adults	August	MRR[2])	BAUR (1988) (2 populations)
Roadside verge, grass, *Symphytum officinale* and scattered *Rubus corylifolius*	Sweden	42.9 and 10.1	> 14 mm	June–August	MRR[2])	BAUR & BAUR (1990) (2 populations)

[1]) Quadrat sampling – [2]) Mark-release-recapture technique

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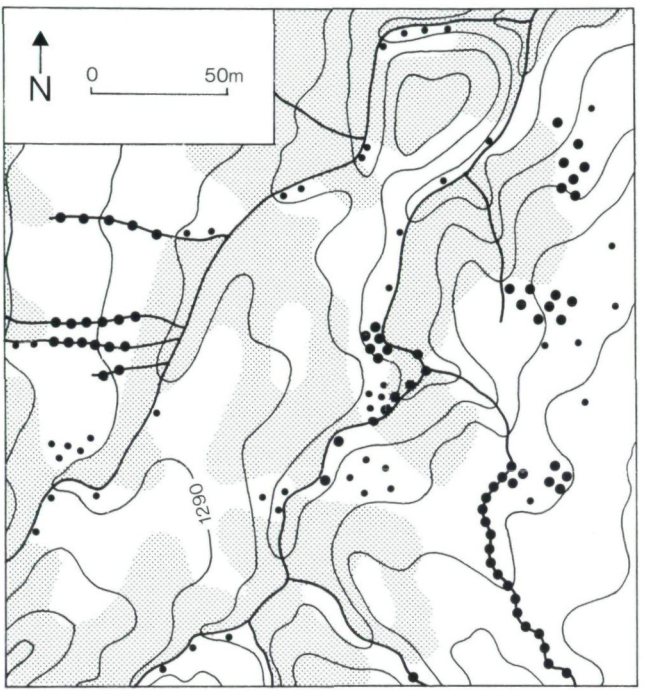

Fig. 3: Spatial distribution of *A. arbustorum* at Potersalp (Alpstein mountains, eastern Switzerland, 1260–1300 m a.s.l.) in summer 1981. Large points represent 200 snails, small ones 50 snails. Shaded areas indicate forest and white areas pasture. Contour interval 5 m.

smaller individuals in a particular habitat. Other authors considered only subadult and adult snails (Table 1). Any mark-release-recapture technique incorporates other sources of bias. SOUTHWOOD (1978) has dealt in depth with the problems associated with these techniques.

A problem shared by all methods that estimate density is the variation in the proportion of snails found in a single sample. Individuals of *A. arbustorum* tend to rest for periods of up to several days buried in the soil (BAUR 1984c, 1986b). The proportion of active snails depends on the season and time of day, the current weather conditions, as well as the weather on the preceding days. In a single examination of a large area, LAMOTTE (1951) assumed that he found 10% of the *C. nemoralis* present, and CAIN & CURREY (1968) estimated that they found 15% in May and June and 10% in midsummer and autumn. When they examined smaller areas, they found 50% of the adults on mild mornings and 15% on frosty ones. In *A. arbustorum*, the recovery rate of marked adults averaged 47.5% (range 20.0–71.4%) after 24 hours in a clearing, and 42.0% (range 33.3–50.0%) along a ditch (A. BAUR & B. BAUR 1993). A proportion of snails remain inactive in the soil even under conditions favourable for activity (A. BAUR & B. BAUR 1993).

Table 1 summarizes population density estimates in *A. arbustorum*, which ranges from 0.1 to 20 adults per m^2. The data available do not allow one to characterize habitat types by any particular snail density.

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In clearings and local stands of ash (*Fraxinus excelsior*) and aspen (*Populus tremula*) in a pine dominated forest near Uppsala in central Sweden, the local population density of *A. arbustorum* ranged from 1.9 to 10.8 adults per m^2 (BAUR 1988). Adult shell size of *A. arbustorum* decreased with increasing local population density (shell volume decreased by 18.6% within the observed range of density). Food is unlikely to be a limiting factor, because *A. arbustorum* is a generalist consuming only a part of the total production of food plants (cf. SPEISER & ROWELL-RAHIER 1991). The accumulation of mucus-trail pheromones may limit the number of snails that can live in a particular area and hence lead to a density-dependent regulation of population size (BAUR 1988). A high density of mucus trails reduces snail activity (in *C. nemoralis*; OOSTERHOFF 1977; CAMERON & CARTER 1979), decreases juvenile growth rate, and reduces the size of adults. Since fecundity (number of egg batches produced and batch size) and egg size are positively correlated with adult shell size in *A. arbustorum* (BAUR 1984a, 1988), this could indirectly lead to a density-dependent control of population size (REICHARDT, RABOUD, BURLA & BAUR 1985; BAUR 1988).

Apart from self-regulation, predation by birds (family Turdidae), toads, shrews, ground beetles and snails as well as parasitism may reduce population density in *A. arbustorum* (for lists of potential predators see WILD & LAWSON 1937; REICHARDT, RABOUD, BURLA & BAUR 1985). In addition, abiotic factors such as drought or extreme cold can cause high, density-independent mortality in snail populations (cf. STÖVER 1973; TERHIVUO 1978). For example, WILLIAMSON (1958) suggested that a shortage of suitable shelter sites under severe conditions can decrease local snail density. However, the relative importance of density-dependent and density-independent mechanisms affecting population size in *A. arbustorum* is unknown.

4. Active dispersal

Rather little is known concerning dispersal in *A. arbustorum*. Studies covering periods longer than 1 year are completely lacking. In four roadside verges in central Sweden, dispersal of marked (adult) *A. arbustorum* averaged 1.5, 1.8, 3.7 and 4.4 m in 3 months (BAUR & BAUR 1990). During the same period, adult *A. arbustorum* moved 4.9 m in a nearby-situated grass-covered clearing. In the eastern Swiss Alps, an average dispersal of 7 m per year was estimated in a 1-m wide and 50-m long belt of nettle and 8 m per year along a ditch (BAUR 1984c, 1986b). In an alpine grassland with scattered scree material, dispersal averaged 12 m per year (BAUR 1984c, 1986b).

Daily movement patterns of individually-marked *A. arbustorum* were recorded in a grass-covered clearing (a two-dimensional habitat) in a coniferous forest near Basel (Switzerland) on 16 consecutive days (BAUR 1991; A. BAUR & B. BAUR 1993). Daily distances moved ranged from 0 to 4.44 m (median value: 0.58 m), and their frequency distribution fitted a function with exponential decay ($y = 21.510\, e^{-0.010x}$; x = distance moved in cm and y = frequency (%)). The snails showed no preference in direction of movement. Further, the directions chosen on

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consecutive days were independent, and the snails moved similar distances in all directions. To examine the effect of habitat form on dispersal, daily movements of *A. arbustorum* were also monitored in a 1 m wide belt of forbs and grass (an almost linear habitat) in a subalpine pasture at Potersalp (eastern Swiss Alps, 1290 m a.s.l.). The distances covered were exponentially distributed and ranged from 0 to 1.57 m (median = 0.40 m). Subadult and adult *A. arbustorum* did not differ in the distances moved. Repeated observations during the day revealed that the snails did not enter the drier surroundings (a mown meadow); individuals that reached the edge of the vegetation belt continued their movements in a new direction within the favourable habitat. The repeated returning at the edges may result in shorter distances dispersed in a linear than in a two-dimensional habitat. This suggests that the pattern of dispersal of *A. arbustorum* is influenced by the form of the habitat (A. BAUR & B. BAUR 1993). Literature data indicate that helicid snails disperse larger distances in two-dimensional habitats than in linear habitats, supporting the results of a simulation study (A. BAUR & B. BAUR 1992, 1993). For example, mean dispersal of *C. nemoralis* was found to be 10 m in 1 year in a grassland in England and 4.7 m along a slope of a river bank (a linear habitat).

Natural snail populations are increasingly fragmented by artificial structures such as roads or agricultural fields, which may act as barriers for gene flow. The effect of road width on dispersal in *A. arbustorum* was examined during one activity season (3 months) in central Sweden (BAUR & BAUR 1990). Subadult and adult *A. arbustorum* were marked in the opposite roadside verges of a paved road (8 m wide), an unpaved track (3 m wide) and an overgrown path (0.3 m wide, partly covered by grass). Subadult and adult *A. arbustorum* did not differ in distances covered at any site. After 3 months, mean distances moved ranging from 1.5 to 4. 9 m were recorded. Several snails covered large distances, the maximum recorded being 14 m. The snails movements were largely confined to the verges along the paved road and the track. No *A. arbustorum* were found either in the adjacent cereal fields or in the pine forest. After 3 months, only one marked snail (0.6%) had crossed the paved road, although 7 of 168 recovered snails (4.1%) moved at least 8 m along the verges, a distance corresponding to the width of the paved road. In the same time interval only 2 marked snails (4.3%) had crossed the track, although 23 individuals (49.0%) moved a distance longer than the track width (3 m). These findings indicate that the paved road and, to a minor extent, the track acted as barriers to dispersal in *A. arbustorum*. By contrast, the path did not appear to influence the snails' dispersal: 41.7% of the recaptured animals had crossed the path during summer. This study was conducted at roads with extremely low traffic densities and consequently low animal mortality due to vehicles. Snail populations separated by paved roads with high traffic densities may be completely isolated from each other.

Arianta arbustorum moves farther during the reproductive season than in autumn shortly before hibernation (BAUR 1984c, 1986b; BAUR & BAUR 1990). Dispersal in other land snail species has been shown to be affected by additional factors including type and height of vegetation (CAIN & CURREY 1968; COWIE

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1980, 1984; BAKER & HAWKE 1990), local population density (GREENWOOD 1974), snail size (SZLAVECZ 1986; BAUR & BAUR 1988) and homing tendency (COOK 1979, 1980). No data are available to test these hypotheses in *A. arbustorum*.

Uphill movements of marked *A. arbustorum* have been repeatedly recorded (BAUR 1984c, 1986b). When placed on an inclined surface, *A. arbustorum* tends to move upwards (BAUR & GOSTELI 1986). Uphill-movements are the result of a negative geotactic orientation behaviour, which allows the snails to compensate for passive downhill transport such as rolling down snowfields and being carried away by avalanches and streams (see Passive dispersal).

Little is known concerning the dispersal capacity of juvenile snails. However, dispersal of newly-hatched (1-day-old) *A. arbustorum* was recorded in a clearing in central Sweden (BAUR 1988). Distances moved averaged 5.8 cm (range: 2–12 cm) in 1 day and increased to 13.8 cm (range : 8–25 cm) in 3 days. The proportion of recovered snails was extremely low (6.7% after 3 days). Therefore the further fate of marked hatchlings was no longer followed.

VISMARA (1983) and ARTER (1985, 1990) examined isozyme patterns and spatial relationships in natural populations of *A. arbustorum*. The allele frequencies are best explained by a functional isolation-by-distance model with streams as the main gene flow paths. The genotypic similarities among populations living at the same stream point to the recolonization of the mountain slopes after the last glaciation by snails from source populations in the tundra of the ice-free lowlands (ARTER 1990).

5. Passive dispersal

Streams and rivers might be the most important agent for passive dispersal of all size classes of *A. arbustorum*. On the bank of the Danube, RICHNOVSZKY (1982) collected living and dead snails which originated from the mountains. This kind of transportation must not end fatally for the snails. For example, *A. arbustorum* can withstand 10–11 h in freshwater at a temperature of 18–20°C (KÜNKEL 1916), and hibernating *Helix pomatia* (LINNAEUS, 1758) with an intact epiphragm survived for 20 days in seawater (DARWIN 1859). The persistence of the snails increased as the water temperature decreased. Furthermore, KÜNKEL (1916) found that eggs of *A. arbustorum* develop normally in freshwater. After torrential rains, the recovery rate of marked *A. arbustorum* was significantly lower in populations along ditches and on stream embankments than in populations living in nearby pastures (BAUR 1984c, 1986b). Many dead snails were observed in mountain streams, and three marked (adult) *A. arbustorum* were found alive 10–30 m downstream from their original sites, one individual on the opposite embankment of a stream 2–3 m wide.

Individuals of *A. arbustorum* were frequently observed to fall from the vegetation and, due to their nearly globular shell, then to roll down steep slopes (BAUR 1984c, 1986b). At places where avalanches start, the soil is often eroded and displaced together with hibernating snails. BÜTIKOFER (1920) described transportations of *A. arbustorum* by avalanches, and on melting remains of avalanches BAUR (1984c, 1986b) found among other snails 230 and 97 individuals

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of *A. arbustorum*, of which 1.7% and 13.4% had survived. Most of the survivors were laying on clods, and the shell aperatures of these snails were closed by an epiphragm. Since the places where the avalanches started were visible, it could be estimated that the snails had been transported up to 350–550 m downhill.

Observations on aerial dispersal in molluscs were reviewed by REES (1965) and DUNDEE, PHILLIPS & NEWSOM (1967). Besides anecdotal reports on transportations by air currents and hurricanes, some land snails have actually been seen attached to legs of insects (e.g. bees and bumble-bees) in flight. However, birds are generally considered to be the most important agent for aerial dispersal in molluscs. REES (1965) summarized more than twenty cases where molluscs have been found at the feet or on the plumage of birds. DARWIN (1859) suggested that transportation of land snails either in the crops of birds from which they may later be disgorged alive, or with nest material, should be possible. Indeed, BIGGS (1968) described the recovery of a living *Succinea putris* (LINNAEUS, 1758) from a pigeon's crop at least 8 h after the bird had died, and *Balea perversa* (LINNAEUS, 1758) and *Trichia hispida* (LINNAEUS, 1758) have been transported on nest material (REES 1965). No records on aerial dispersal of *A. arbustorum* are so far available.

6. Neighbourhood size and effective population size

A continuous distribution of snails on a mountain slope does not insure the absence of genetic differentiation by genetic drift and amplification of this by interdeme selection (selection pressures can change within short distances). The amount of differentiation at a locus as a consequence of genetic drift depends on the effective population size of the panmictic units (i.e. deme size) or neighbourhoods (the regions surrounding individuals within which the gametes which produced them may be considered to have been drawn at random; cf. WRIGHT 1969). In any population in which the rate of dispersal is small compared with the area occupied by the population, isolation by distance will prevent panmixis and the effective population size will be less than the actual number. WRIGHT (1969) has provided a model for evenly distributed populations (the neighbourhood size concept).

Some confusion has arisen in the literature about the distinction between the concepts of neighbourhood and effective population size. For a discrete, panmictic population, the effective population size is the size of an idealized population equivalent genetically to a real one. This concept is not applicable to a continuously distributed population in which neighbourhood size, combining both density and dispersal within the population, is appropriate. However, many real populations will probably be intermediate in structure.

WRIGHT (1969) defined the neighbourhood size for a two-dimensional population as

$$N = 4\pi s^2 d$$

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in which N is the number of organisms in the neighbourhood area, s^2 is the variance of dispersal along a single axis, and d is the density of the breeding population. The corresponding formula for a linear population is

$$N = 2\sqrt{\pi}sd.$$

Using these formulae, a neighbourhood size of 5600 was estimated for a two-dimensional population of *A. arbustorum* in central Sweden and of 388 individuals for a linear population in the eastern Swiss Alps. The neighbourhood area of the two-dimensional population corresponds to a circle with a diameter of 32 m. Using the data of LAMOTTE (1951), WRIGHT (1969) estimated a neighbourhood size of 2800 for *C. nemoralis* and a corresponding neighbourhood area consisting of a circle with 40 m diameter.

The effective population size (N_e) may depart from the neighbourhood number (N) under certain conditions (MURRAY 1964; WRIGHT 1969; GREENWOOD 1974). These include asymmetry in investment in female vs. male reproductive function, non-random fertilization of eggs, non-random dispersal, changing population size and non-random variation in lifetime reproductive success. Estimates of effective population size that take into account some of these factors are available for *C. nemoralis* (N_e ranges from 95 to 6000; GREENWOOD 1974, 1976), *Theba pisana* (MÜLLER, 1774) (N_e ranges from 115 to 4130; COWIE 1984), and *Helix aspersa* MÜLLER, 1774 (N_e ranges from 15 to 215; CROOK 1980). However, no similar estimates are available for *A. arbustorum*.

7. Concluding remarks

This review indicates that, compared to the large amount of taxonomic and systematic work, relatively little research has been done on the ecology of natural populations of *A. arbustorum*. To understand the underlying causes of morphological and isozyme differences among populations, detailed knowledge of population size and spatial structure and the extent of gene flow are important.

Given the heterogeneity of an alpine landscape, one must get information on the size of sampling areas. It is possible that large populations (which easily yield large sample sizes) come from larger and hence more variable areas than do smaller ones. Estimating neighbourhood size is a first step towards reducing this source of error.

Of the factors which may cause changes in gene frequencies in snail populations, gene flow is probably the least well studied. There is an urgent need for long-term studies that examine snail dispersal among populations and whether dispersing animals breed successfully at the novel sites. This kind of information could be used in simulation studies, which might provide further insight into possible colonization paths and other events of differentiation.

CAIN (1983) concluded in his review on the ecology and ecogenetics of terrestrial molluscan populations that 'the ecology and behaviour of terrestrial molluscs are far from simple; that major features of their population biology can vary over a few feet, as can selection; and that the results of temporal surveys are of special importance in interpreting apparently enigmatic variation!' *A. arbustorum*

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exhibits a great deal of variation in alpine populations. Complex and perhaps unique explanations might be needed for different situations, and the relative importance of the various mechanisms causing and maintaining the observed pattern may vary from population to population. Well-designed field studies will help to bring new light into this most interesting topic.

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