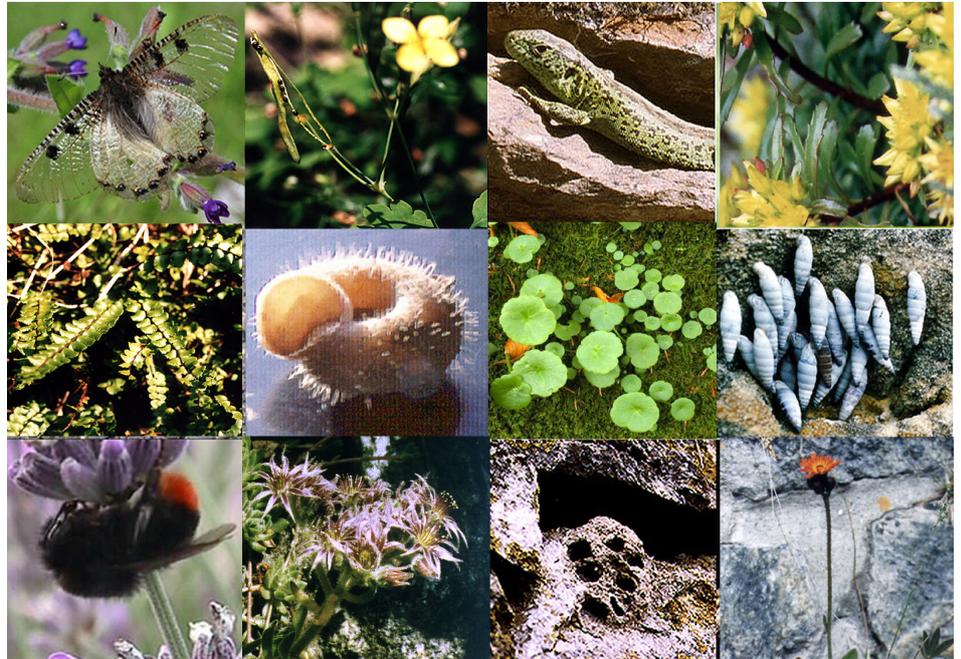


Ecology of dry stone walls

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Dry stone walls offer a wealth of different habitats. Hot and cold, dry and humid, shady and sunny places are close together in a very small space. A multitude of insects, spiders, snails, reptiles and amphibians find ideal retreat, hunting and wintering possibilities in the crevice system of a dry stone wall. Many of the animals and plants have specialised in living on dry stone walls. Snails have adapted the shape of their houses to the narrow crevices. In plants, strategies for regulating the water balance or seed dispersal can be observed. The conservation of dry stone walls therefore means the preservation of habitats and thus contributes to the preservation of biodiversity.

1. Drystone walls, artificial habitat

If you look around to see which natural elements a dry stone wall corresponds to, the comparison with rock faces and scree slopes is obvious. As with rock walls, there are gaps and cracks, analogous to the joints in masonry. The network of joints between the stones of a dry stone wall corresponds to the widely ramified cave world as it occurs in scree slopes in the mountains. A dry stone wall represents a mosaic of different habitats in a confined space. The character of these habitats depends on the type of wall (retaining wall or free-standing wall), age, type of rock (acid or alkaline environment), geographical location (orientation of the wall surface) and microclimatic conditions.

2. Microclimate on drystone walls

2.1 Temperature conditions on dry stone walls

The temperatures that prevail on dry stone walls are determined by the orientation of the wall, shading and the type of wall (retaining wall or free-standing wall). Walls facing north and east receive little solar radiation. On them it is rather cool, without large temperature fluctuations. The situation is different with south- and west-facing walls. In summer as well as in winter the sun warms the wall. In summer the stone surface is heated up to 70°C and even in winter there are mild temperatures during the day, as the low sun shines almost perpendicularly on the surface of the wall. But at night the stone surface cools down considerably. South- and west-facing walls therefore show large temperature fluctuations on the surface (30 - 50°C during the day). Inside the wall, on the other hand, there are balanced temperatures with only slight fluctuations. A dry stone wall therefore has a balancing effect on the climate of its immediate surroundings. Heat stored in the stones during the day is conducted into the wall at night or radiated outwards.

2.2 Moisture conditions on dry stone walls

Water is one of the most important factors determining the species composition and growth of plants on dry stone walls. More moisture means more vegetation and a more balanced climate on the wall surface, more vegetation also means more moisture, larger plants, more mosses, more ferns.

- Freestanding wall (see Fig.1)
The south side dries faster, the north side remains moist longer. Both sides have in common that the moisture supply in the wall is relatively low due to lack of contact with the earth. Only in the foundation area of the wall, the contact point between masonry and earth, is there permanent moisture. On the two opposite wall surfaces, different plants settle, depending on whether they prefer shade or sunny locations.

- Retaining walls (see Fig. 2)
The soil supported by the wall ensures a constant influx of moisture. A damp, balanced climate prevails within a dry-walled retaining wall. If the surface of the wall is exposed to strong sunlight due to a favourable orientation, a combination of different habitats results: The surface is dry and with large temperature fluctu-

ations, the interior of the wall is rather cool and humid with a balanced temperature.

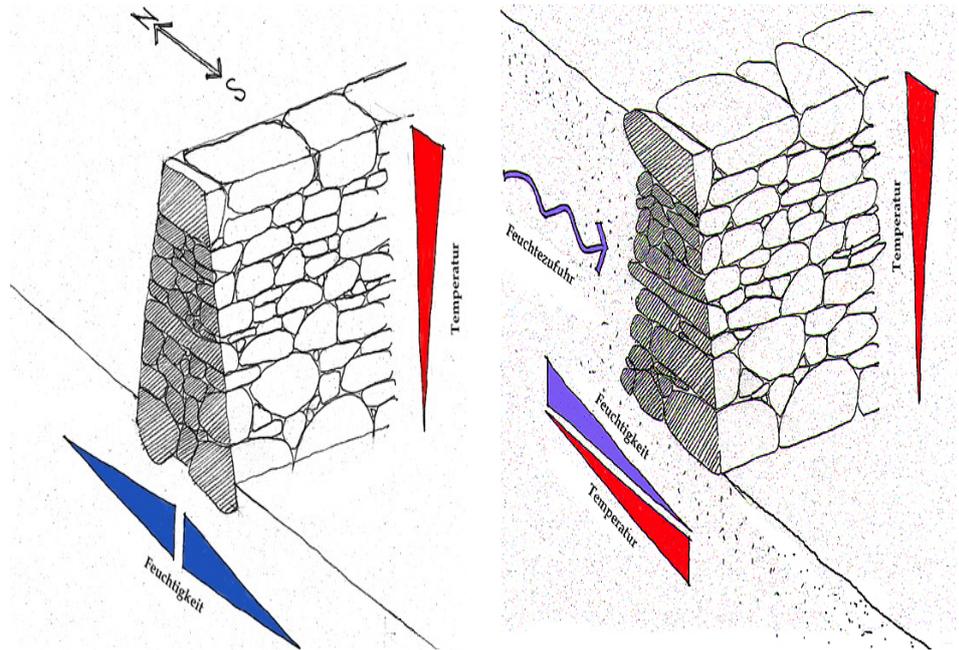


Figure 1, left:
Free-standing wall,
moisture and temperature
conditions.
Figure 2, right:
Retaining wall, moisture
and temperature conditions.

3. Colonization by plants and animals

3.1 Sequence of colonization by plants

The colonisation takes place in a fixed sequence: First, the stones exposed to the weather are colonised by bacteria which penetrate into pores and crevices. With the exception of a slight change in colour of the stone surface, nothing is yet visible to the naked eye. After dying, the bacteria leave carbon and nitrogen behind. These substances form the prerequisite for algae and fungi to settle. Algae, mostly blue or diatom algae, are present on all wall surfaces, but prefer the less sunny, weather-protected east and north sides of walls. After many years, as soon as the climatic conditions allow, a crust-like growth of different structure and colour can be seen here and there. These are lichens, a symbiosis (biocoenosis) of algae and fungi. Lichens grow very slowly, usually only 1 to 4 mm per year. The surface of the stone is first covered by crustal lichens, the substrate is mechanically and chemically attacked. Crust lichens are replaced by leaf lichens. Lichens can reach an age of several hundred years. Contrary to the common belief that algae only grow in a clean atmosphere, there are also species that can exist in polluted air (usually crust lichens).



Figure 3:
Pioneers of wall colonization: lichens

In the course of the years the stone surface is more and more populated. Dead parts of the lichens break off, collect on ledges and in stone crevices and rot. These small earth depots allow mosses to grow. There are also numerous species of mosses, each of which is specialized for certain locations. Interesting are the drought resistant mosses. They survive long dry periods by slowing down their metabolism considerably. As soon as rain falls, such mosses quickly swell up again. The cus-

Figure 4:
Moss follows lichens in the colonization sequence



Figure 5:
Last stage of vegetation: vascular and flowering plants grow from moss cushions and soil depots



hion shape of the mosses favours water storage, the moss cushion acts like a sponge and reduces water evaporation.

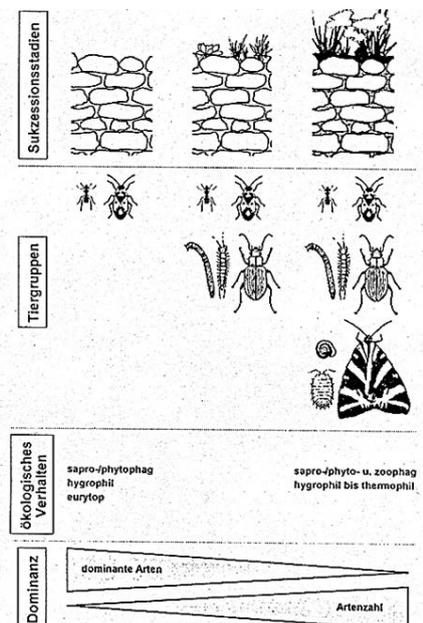
Vascular plants only settle very late, when algae, lichens and mosses have prepared the habitat and sufficient soil has accumulated on ledges and in crevices. Pioneer plants appear first, including grasses, ferns such as wall rue and flowering plants such as cinnamonwort, glasswort, sedum, spring hunger flower and houseleek. Later other plants also settle in the area. The colonization process is completed by the colonization of woody plants, which damage and destroy the wall by their roots and the thickness of the trunk. It is estimated that the full development of the wall vegetation takes 100 - 500 years.

3.2 Colonisation by animals

The colonisation of a wall consisting of newly broken, 'sterile' stones is carried out from neighbouring habitats. The decisive factors here are the animals' radius of action, how fast they can move and what demands they make on the habitat. This makes it clear how important it is for newly built walls to have a diverse environment and for old walls to be populated

Pioneers are ants and bugs, both are very mobile. Ants have an important function in spreading plants along walls. Even at an early stage the wall is also used by reptiles (lizards, snakes) and mammals (mice). Again, the older the wall, the richer the flora and fauna, the greater the likelihood of many such animals appearing.

Figure 6:
Insect colonization sequence: The older the wall and the more humus in the crevices the greater the number of animals and species.
Source: [20]



Limbed animals (centipedes, millipedes and beetles) are not so keen on migration. They need more time to colonize.

Only in older dry stone walls are animals with a very small radius of action or very special requirements to be found. Snails are dependent on moisture and humus and move very slowly. Isopods depend on sufficient moisture and humus and the caterpillars of some butterflies, which are specialized on food plants (e.g. lichen, sedum) found on walls, do not colonize the wall until the appropriate plant is available.

4. Use of drystone walls by plants and animals

Winter quarters

Amphibians and reptiles retreat into the deep crevices and cavities of the wall and bury themselves in humus and sand in the frost-free area (toads, salamanders, lizards including blindworms, snakes). Bumblebee queens and butterfly caterpillars and pupae spend the winter in frost-free crevices of walls. Hedgehogs like to use ground-level hollows filled with leaves as winter quarters.

Retreat / protection area

Nocturnal animals such as woodlice or amphibians like to retreat during the day into the dark and damp crevices of the wall where they find shelter.

Hatchery

- solitary bees / wasps: clay, sand joints, nests on stone surface.
- Some butterfly caterpillars like to visit dry stone walls for pupation. They include whites (Pieridae) and foxes (Vanessae). The whiteflies tend to attach themselves to vertical surfaces. Foxes under stone ledges.
- Heat-loving small mammals: mice.

Food basis, hunting ground

Dry stone walls are home to numerous predators, e.g. spiders, reptiles and various insects. Visitors from neighboring habitats (e.g. butterflies, lacewings, solitary bees and wasps, beetles and bugs), which need the wall as a resting and warmth place, are the prey of these hunters.

Warmth dispenser

Niche location in a foreign environment

Various plants, which are actually native to the mild climate of the Mediterranean, find favorable living conditions on south-facing dry stone walls.

5. Adaptation of plants to the climate on dry stone walls

In free-standing walls, rain, dew and meltwater are the only sources of moisture. Plants that grow on such walls must be able to survive long periods of drought. These drought-resistant plants (xerophytes) have developed various survival strategies for this purpose.

- Overproportional root system

Different plants form a root system that is disproportionately large compared to the size of the plant (example: cinquefoil, *Potentilla verna*).

- Small surface, sponge structure

The smaller the surface of the plant is, the less water it loses. There are several ways to minimize the surface area: Some plants have a typical cushion shape, which, analogous to a sphere, gives a minimal surface area for a given volume. Examples for such plants are mosses and plants that form a cushion, e.g. different saxifrage species. These cushions can store water like a sponge (mosses up to 400% of dry weight). Other plants reduce their surface only when there is a real danger of dehydration. They fold the leaves together to keep them out of the sun's rays or roll the leaves up, which again results in the cushion or ball shape described above. Examples of such plants are all grasses that grow on walls and some ferns. The grasses fold up the leaves when dry, the writing fern (*Ceterach officinarum*) rolls up the leaves when dry.



Figure 7:
Cushion and sponge structure of moss cushions for water storage.

Figure 8:
In orange hawkweed (*Hieracium aurantiacum*) leaves, water evaporation is reduced by leaf hairs. It leads to a slowed air flow over the leaf surface.



Reduction of the drying air flow

The fine hairs that the leaves of some plants have have the purpose of slowing down the airflow over the leaf surface. This reduces evaporation. An example of plants with such leaves is the orange-red hawkweed (*Hieracium aurantiacum*) (see Fig.8).

- Bridging of dry periods
Some annual plants bridge the hot, low-precipitation summers by flowering very early and forming seed heads. The seeds, insensitive to drought, remain lying and germinate as soon as the moisture supply is large enough again. Examples of such plants are pod cress (*Arabidopsis thaliana*), tangled hornwort (*Cerastium glomeratum*), spring hunger flower (*Erophila verna*) and all saxifrage species (*Saxifraga*).

Figure 9:
The fleshy leaves of the wall pepper (*Sedum*) store water. They are covered with a wax layer to protect against excessive evaporation of water.



Special surface

Excessive water loss can also be prevented if the leaf surfaces are waterproofed. Some plants, usually of a typical blue-green color, have a leaf surface which is coated with a wax-like coating. Often such leaves are also distinctly "leathery". Examples of such plants are Venus navel (*Umbilicus rupestris*), goose thistle (*Sonchus oleraceus*), saxifrage (*Saxifraga*), woad (*Isatis tinctoria*) and ivy (*Hedera helix*).

tinctoria) and ivy (*Hedera helix*).

Figure 10:
The hygroscopic sap of the celandine (*Chelidonium majus*).



Spezieller Pflanzensaft

The sap of some plants is composed in such a way that water loss through evaporation is minimized. Due to a high salt content, the sap is water-retaining (hygroscopic), i.e. it strives to attract moisture from the environment. An example of such a plant is the celandine (*Chelidonium majus*), which contains an orange-colored milky liquid (cf. Fig.10).

- Water storage
Some plants store water to survive dry spells. Fleshy leaves contain the water which helps to bridge heat and dry periods. Such plants include all species of wall peppers (*Sedum*) and houseleeks (*Sempervivum*) (see Fig.9).

Often, plants use several of the water-saving strategies simultaneously.

6. Adaptation of animals to the drystone wall habitat

Some snail species have adapted their shell shape to live in narrow crevices and on vertical surfaces. These include the Closemouth Snails (*Clausilia*) and the Stone Pickers (*Helicigonia*). Their shells are either flattened or elongated pointed in order to be able to move in narrow crevices or crawl on vertical surfaces (cf. Fig.11).



Abbildung 11:
Door snails (*Clausilien*)

7. Sociology of Plants

The vegetation of a site reflects the living conditions of a site (climate, subsoil, nutrients, etc.). Plant sociology describes the plants that occur together under the same site conditions. For drystone walls, these are *Asplenietea* communities. The natural location of these communities are rock surfaces and crevices. However, they can also colonize the man-made "substitute habitats" wall or stone wall.

Site conditions can be described among others according to the following criteria:

- Temperature
(cold pointer, cool pointer, heat pointer, heat pointer)
- Water
(dry pointer, fresh pointer, wet pointer, wetness pointer, change water pointer)
- Light
(shade-loving, partial shade-loving, sun-loving)
- Nutrients and bases
(nutrient-poor, moderately nutrient-rich, nutrient-rich, excessively nutrient-rich)
- Soil
(acid indicator, moderate acid indicator, base indicator, lime indicator)

Some characteristic plant communities can also be described on dry stone walls. The main differences between the individual communities are due to the different soil / subsoil and secondarily to influences such as insolation and temperature. In general, societies on calcareous sites are much more species-rich than on calcareous-poor sites. Rock crevice and wall joint societies are long-lived, distinctly permanent societies that can maintain their place for centuries. The development of such a society on a new wall usually takes 100 to 500 years.

Listed below are the major plant communities with their respective associated plant species.

Asplenieta trichomanis (Class)
Crevices and wall joint societies

Class character species:
 Braunstieliger Streifenfarn (Asplenium trichomanes)
 Schriftfarn (Ceterach officinarum)
 Rosen-Steinbrech (Saxifraga decipiens)

Potentilletalia caulescentis (Order)
Limestone crevice communities

Order character species:
 Zimbelkraut (Cymbalaria muralis)
 Mauerraute (Asplenium ruta muraria)
 Mannschild (Androsace lactea)
 Jura-Streifenfarn, Fluhfarn (Asplenium fontanum)
 Bergseidelbast (Daphne alpina)
 Blaugrünes Rispengras (Poa glauca)
 Stengel Fingerkraut (Potentilla caulescens)
 Zwerg-Kreuzdorn (Rhamnus pumilus)
 Trauben-Steinbrech (Saxifraga paniculata)
 Drehzahnmoos (Tortula muralis)
 ??Moos (Homalothecium lutescens)
 ??Moos (Ctenidium molluscum)

Androsacetalia vandellii (Order)
Silicate rock crevice society

Order character species
 Nordischer Streifenfarn (Asplenium septentrionale)
 Deutscher Streifenfarn (Asplenium alternifolium)
 Himmelsherold (Eritrichium nanum)
 Felsenrapunzel (Phyteuma scheuchzeri)
 Goldenes Frauenhaarmoos (Polytrichum piliferum)
 ??Moos (Ceratodon purpureus)
 ??Moos (Racomitrium canescens)

Potentillion caulescentis (Community)
Cinquefoil rock crevice society
Limestone crevice communities,
sunny locations

Community differential types:
 Lerchensporn (Corydalis lutea)
 Langgestielter Mannschild (Androsace lactea)
 Zwerg-Gänsekresse (Arabis pumila)
 Dolomit-Streifenfarn (Asplenium seelosii)
 Felsen-Schaumkresse (Cardaminopsis petraea)
 Stachelspitzige Segge (Carex mucronata)
 Immergrünes Felsenblümchen (Draba aizoides)
 Ladiner Hungerblümchen (Draba ladina)
 Sauters Felsenblümchen (Draba sauteri)
 Filziges Felsenblümchen (Draba tomentosa)
 Alpen-Schwingel (Festuca alpina)
 Schmalblütiger Schwingel (Festuca stenantha)
 Hasenohr-Habichtskraut (Hieracium bupleuroides)
 Niedriges Habichtskraut (Hieracium humile)
 Kugelschötchen (Kerneria saxatilis)
 Mannschild-Miere (Minuartia cherlerioides)
 Felsen-Miere (Minuartia rupestris)
 Ostalpen-Fingerkraut (Potentilla clusiana)
 Burser-Steinbrech (Saxifraga burseriana)
 Dickblättriger Mauerpfeffer (Sedum dasphyllum)
 Felsen-Baldrian (Valeriana saxatilis)
 Gelber Ehrenpreis (Veronica lutea)

Androsacion vandellii (Community)
Ciliated fern rock crevice society
Silicate rock crevice societies,
sunny locations

Community character types:
 Nordischer Streifenfarn (Asplenium septentrionale)
 Vandellis Mannschild (Androsace vandellii)
 Alpen-Leinkraut (Artemisia mutellina)
 Schwarzstieliger Strichfarn (Asplenium adiantum-nigrum)
 Felsen-Berufkraut (Erigeron gaudinii)
 Schöterich (Erysimum rhaeticum)
 Weißliches Habichtskraut (Hieracium intybaceum)
 Rote Felsen-Primel (Primula hirsuta)
 Rosenwurz (Rhodiola rosea)
 Moosteinbrech (Saxifraga bryoides)
 Rosettensteinbrech (Saxifraga cotyledon)
 Sponheimer Steinbrech (Saxifraga sponhemica)
 Alpenwimperfarn (Woodsia alpina)
 Südlicher Wimperfarn (Woodsia ilvensis)
 Rostroter Wimperfarn (Polytrichum piliferum)
 ??Moos (Ceratodon purpureus)
 ??Moos (Racomitrium canescens)

Cystopteridion fragilis (Community)
Bladder fern rock crevice society
Limestone crevice communities,
shady locations

Verbandcharakterarten:
 Blasenfarn (Cystopteris fragilis)
 Grünstieliger Streifenfarn (Asplenium viride)
 Grüner Streifenfarn (Asplenium fissum)
 Kurzhäufige Segge (Carex brachystachys)
 Alpenblasenfarn (Cystopteris regia)
 Moos-Nabelmiere (Moehringia muscosa)
 Hirschzungenfarn (Phyllitis scolopendrum)
 Zierlicher Wimperfarn (Woodsia pulchella)

Asarinion procumbentis (Community)
Silicate rock crevice societies,
shady locations

Verbandcharakterarten:
 Billots Streifenfarn (Asplenium billotii)
 Serpentinfelsen:
 Braungrüner Serpentin-
 streifenfarn (Asplenium adulterinum)
 Serpentin-Streifenfarn (Asplenium cuneifolium)

Explanation of terms:

- Order: multiple order character types enclose different classes into one order
- Class: Several class character species unite different associations to one class
- Character species: plants that show a strong attachment to the respective plant community

8. Construction measures to support colonization by plants and animals

The basis for the colonization of dry stone walls is the unobstructed connection of the wall body to the surrounding habitats and to the soil in the area of the foundation and the back of the wall. It is important that no concrete foundation is used and that the back of the wall is not separated from the soil (e.g. by a fleece) (cf. Fig. 12). Walls need a green foot and a green head. This serves the animals as a food base, a hunting ground and a locomotion area.

Old stones that have already been exposed to the weather are usually already overgrown with algae, lichen and moss. The use of such stones accelerates the process of wall colonization. If the whole wall cannot be built from old stones, old and new stones should be mixed.

When rebuilding old, existing walls, it would be ideal if old sections of wall were left standing between new sections of wall (cf. Fig. 13). From these old, already colonized wall sections, plants and animals can migrate into the new walls. The same applies to the immediate surroundings of the wall. The richer and more varied the vegetation of the areas adjacent to the walls, the larger the group of animals that can make use of the wall. A dry stone wall located directly on a busy road will be colonized more slowly and by fewer animals than a wall located in the middle of extensively used rough pastures.

Figure 12, left:
The connection from the wall body to the soil must be ensured so that animals can burrow in for hibernation and reproduction

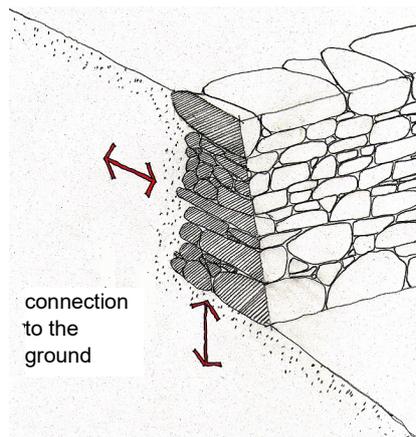


Figure 13, right:
Colonization of new wall sections from adjacent old wall sections.

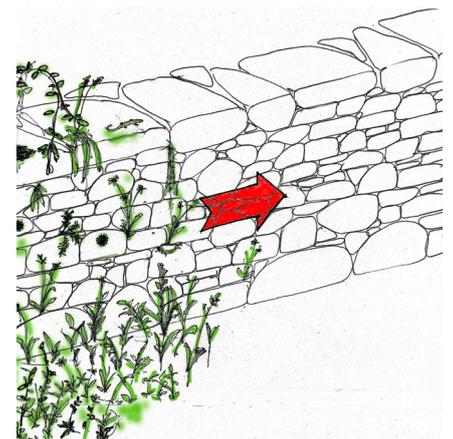
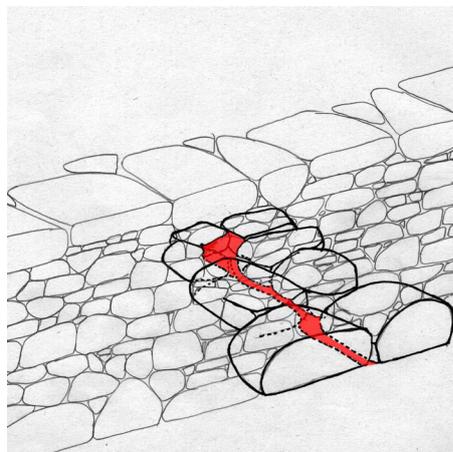


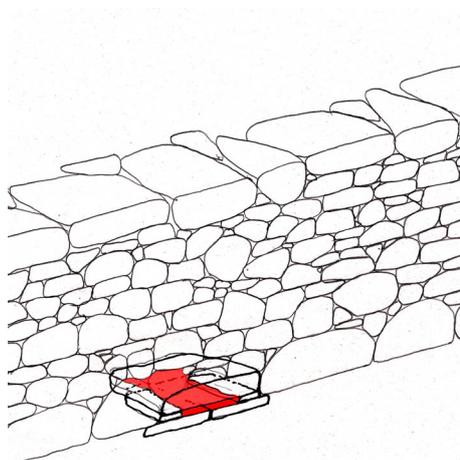
Figure 14:
Hibernation burrows for reptiles



Reptiles (lizards and slow worms, snakes).

South-oriented walls. Alternating planting (mosaic of sunny and shady places) rather outer surface of the wall, in winter the inside of the wall is also important as a place for hibernation (frost-free stone and earth caves behind retaining walls, which are not accessible to rats, polecats, stoats).

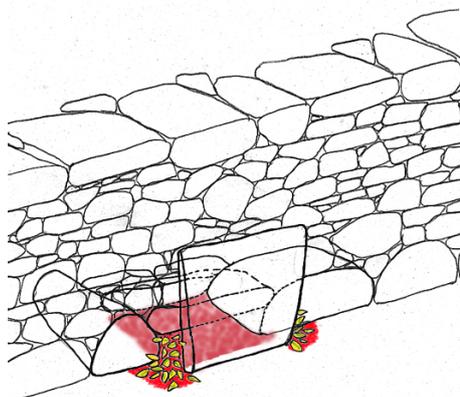
Figure 15:
Retreat crevices for
amphibians



Amphibians

Toads, as nocturnal animals, like to sit in shallow crevices during the day, where their abdomen and back are in contact with the floor and ceiling. The climate in the crevice should be rather cool and humid, thus corresponding more to walls oriented to the north and east. For toads, therefore, stone slabs could be built into the wall near the floor, between which a slit of about 4 to 5 cm is left open. Water areas near the wall are important.

Figure 16:
Hollows for hedgehogs



Hedgehog

South to west facing walls. Installation of dry, leaf-filled hibernation burrows at the base of the wall that can be opened for cleaning.

Figure 17, left:
Nesting aids for insects

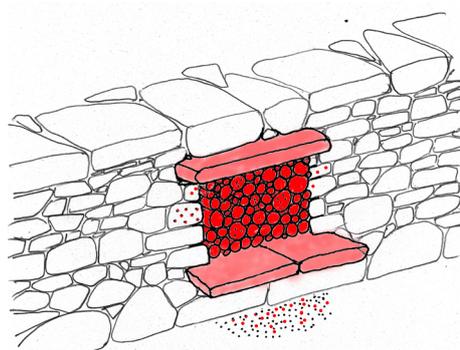
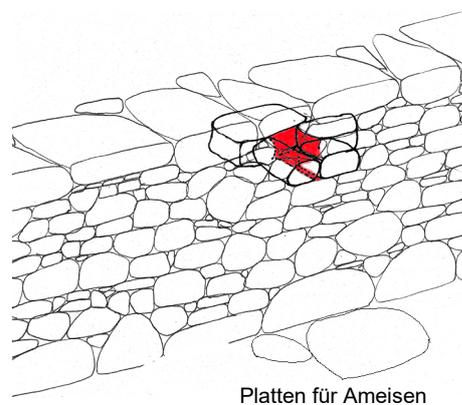


Figure 18, right:
Nesting aids for birds,
bats and ants



The settlement of insects is best supported with a rich supply of plants in the vicinity of the wall. These food plants increase the number of insects that visit the wall in addition to the plants. This also allows the population of predatory insects (for example, spiders) to develop. The use of fine material (sand, clay, humus) in the dry stone wall, which would accelerate the colonization of the wall by many insects and snails, cannot be re-

commended because the risk of frost damage to the stones is quite high. However, supporting measures can be taken for some insect species:

- Solitary bees and wasps
South oriented walls. Sand surfaces, clay surfaces. Fill wall niches with wood, drill pencil-thick holes in the wood and stones. Weather protection.
- Bumblebees
Installation of wall cavities in south-facing walls. Filling in fine nesting material (wood wool, hay). Covering the nest cavity with a large board to prevent water from entering. If possible, construct (e.g., under capstones) so that it can be opened. Important: Rich supply of flowering plants in the vicinity of the wall.
- Ants
South-facing walls, flat stones at the base of the wall or as wall coping.

Bats

South to west facing walls. Installation of straw-filled cavities at the top of free-standing drystone walls.

Birds, cavity breeders

(wheatear, dipper, wagtail, titmouse, hoopoe)

Installation of nesting holes and niches in walls

- Tits (Parus) (Coal, Blue and Coal Tit) in wall cavities (access D: 3 cm base 12 x 12 cm, not too deep inside the wall, in the upper half of the wall).
- Hoopoe (Upupa epops), in wall cavities (access D: 5-8 cm, base 20 x 20 cm, height 15-20 cm, depth 20-40 cm. Height entrance about 50 cm from ground). The hoopoe uses orchards as well as sunny meadows, pastures and fields as habitat. As a result of deforestation of many high-stem orchards and decline of extensively used fields, the hoopoe is threatened in Switzerland.
- Dipper (Cinclus cinclus), in wall niches directly adjacent to water bodies (e.g. in bridge restores).
- Brook Wagtail (Motacilla), in wall niches directly next to water bodies (e.g. in bridge restorations).

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