Prostrate Perennial Knawel

Its ecology and conservation

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BACK FROM THE BRINK

Image: Alex Hyde

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1. Morphology, Identification, Taxonomy & Genetics

1.1. Morphology and Identification

Prostrate perennial knawel *Scleranthus perennis* ssp. *prostratus* is a biennial (sometimes annual) or short-lived perennial of the family Caryophyllacae growing to 20cm with woody basal parts and some sterile shoots at flowering time. Stems are procumbent to slightly ascending bearing linear leaves arranged in opposite pairs fused at the base. Leaves 3-5 (-7)mm, glabrous or only slightly ciliate, often curved to one side of the stem and with axillary leaf-clusters; bracts shorter than the flowers (Clapham *et al*. 1987). Flowers, arranged in dense terminal or axillary cymes (Sell Svennson 1985), are greenish-white and can be inconspicuous; they usually have 5 sepals but no petals. Sepals are subacute to obtuse, with a white border (nearly as wide as green central part) approximately 0.3-0.5mm wide, tips parallel or incurved over ripe achene; there are ten fertile stamens, two styles, and the achene (including sepals) is 2-3(3.5)mm long. 2n=22. (Stace 2010).

In the UK, perennial knawel has two sub-species, one of which *Scleranthus perennis* ssp. *perennis* is confined to a single locality in Radnorshire, has ascending to erect stems; achene (including sepals) (3)3.5-4.5mm, (Stace 2010), and therefore presents no identification problems with the Brecks sub-species prostrate perennial knawel *Scleranthus perennis* ssp. *prostratus*.

The close relative annual knawel *Scleranthus annuus* is an annual or biennial with a slender tap-root and one or more branched or decumbent stems; it is sometimes found with Prostrate perennial knawel. Prostrate perennial knawel differs in the presence of woody basal sections, is usually more robust and more glaucous, becoming reddish, and the sepal margins are wider and whiter than annual knawel. In fruit, the perigynous tube is hairy with ten shallow furrows, as opposed to the more deeply furrowed and glabrous tube of annual knawel (Clapham *et al*. 1987).

1.2. Taxonomic considerations

Prostrate perennial knawel is endemic to England, where it is restricted to the Breckland of East Anglia. Hybrids with Annual knawel have been reported in the Breckland (BRPD 1907, 1958) but never confirmed; according to the BSBI database, by 2021 there were no confirmed examples of hybrids with Annual knawel in the UK. Such hybrids have been reported from Scandinavia (Stace 1975) and France (Tela Botanica 2021); hybrid flowers have a conical, stunted perigynous zone; sepals vary within an individual flower, some with wide, others with narrow white margins; anthers empty or with abortive pollen and usually sterile (Ulla-Maj Hultgård in Jonsell (ed.) 2001).

1.3. Genetic Implications

No studies on genetic diversity within this species have been carried out.

2. Distribution and Current Status

2.1. Europe and the World

Prostrate perennial knawel is endemic to England but, according to the Global Biodiversity Information Facility (2021), its 'parent' species, perennial knawel, is endemic to Europe, widespread north to about 66° N and only absent from areas of great altitude, southwest Spain/Portugal, and coastal regions of the Mediterranean. It is also known from Turkey. Perennial knawel has also been introduced to USA and Canada.

2.2. England and the UK

Prostrate perennial knawel is considered Endangered at a Great Britain level (Cheffings & Farrell 2005) and in England (Stroh *et al,* 2014).

According to Clapham *et al* (1987), it is a rare plant of arable fields, open ground and of short semi-closed vegetation on dry non-calcareous sand. Our observations in the Brecks show it is also associated with areas where vehicle movement, livestock, and rabbit activity limit competition and create bare areas required for seedling establishment. Competition may also be suppressed by compression of the soil, especially by trampling, as the plant seems able to cope with a hard crust forming at the surface. They also lead to the conclusion that there is some tolerance of base chemistry. The species is not known from exclusively acid areas and all known sites have traces of chalk in the soil, even if extensively leached out.

The plant has only been recorded from the vice-counties of West Suffolk, East Norfolk and West Norfolk. Prior to 1970 it was recorded as a native in six hectads (10km squares), in the period 1987 to 1999 as native in two hectads and as an alien in 2 hectads (Preston *et al*. 2002). Historically, described as rare in Norfolk (Nicholson 1914) and very rare in Suffolk (Simpson 1982) it has been recorded from a total of 25 sites (Table 1), never appearing at more than six in any one year (Crompton, 1974-1986).

It was last recorded in West Norfolk in 1961 at Weeting Heath, and previously in 1943 at Barnhamcross Common. Away from Breckland it occurred at Snettisham Beach before flooding in 1953, and in East Norfolk at Cley in 1954 (Beckett *et al*., 1999). In West Suffolk it was recorded sporadically and has the only three remaining native sites in Breckland, at Eriswell (two) and RAF Lakenheath. Successful introductions have taken place at Deadman's Grave (Icklingham), at Thetford Heath and Center Parcs (Elveden), plus another across the border in West Norfolk, north of Santon Railway Crossing. A further two attempts at Mildenhall Woods and West Stow Country Park were unsuccessful (Sandford & Fisk, 2010). A further five translocations have occurred under the Shifting Sands Project, with plants introduced at two locations on Santon Heath, again to Lakenheath Warren after the older introduced stand there failed, an accidental reinforcement at Lord's Well field (the plant was believed extinct after repeated null surveys but was re-found immediately after reintroduction work), and at Barnhamcross Common, on land prepared under a different project.

Table 1: Sites where prostrate perennial knawel has been recorded, with date of first and last record. The table includes sites at which prostrate perennial knawel has been (re)-introduced (table sorted by first year of record). Extant sites are highlighted in green.

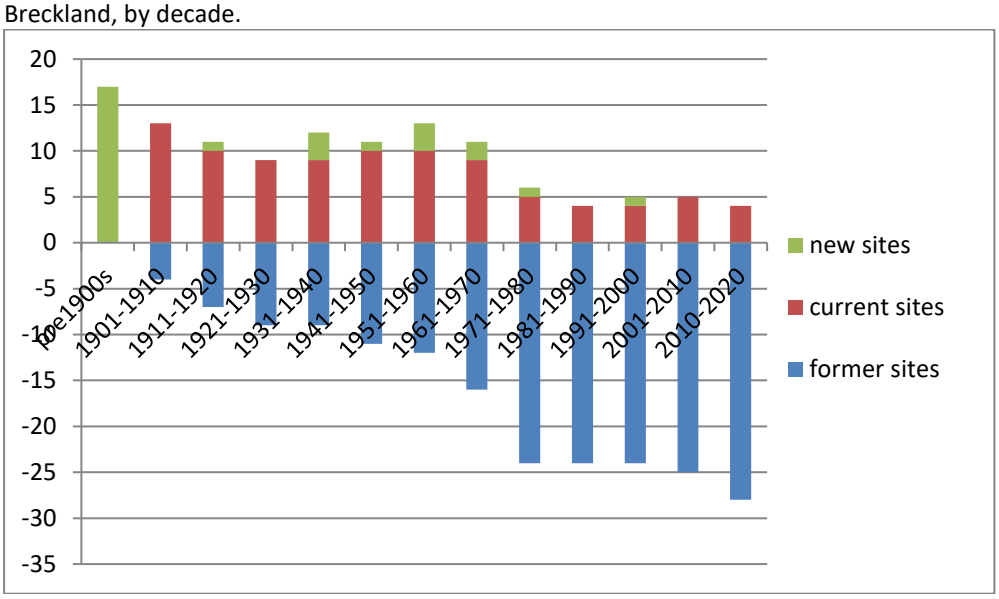
Vice-County	Site	Status	Year of first record	Year of last record
26 West Suffolk	Elveden	Native / Extinct	1677	1910
28 West Norfolk	Barnhamcross Common	Native / Extinct: (Reintroduced)	1738	1971 (2021)
26 West Suffolk	Icklingham, Rampart Field Area	Native / Extinct	1770	1912
26 West Suffolk	Culford	Native / Extinct	1774	1883
26 West Suffolk	Mildenhall	Native / Extinct	1827	1934
26 West Suffolk	Barton Mills, near St. Helena Cottages	Native / Extinct	1827	1974
26 West Suffolk	Icklingham Plains	Native / Extinct	1828	1953
28 West Norfolk	Snettisham	Native / Extinct	1834	1945
27 East Norfolk	Cley	Native / Extinct	?	1954
26 West Suffolk	Eriswell	Native / Extinct	1846	1949
26 West Suffolk	Icklingham, Private Road	Native / Extinct	1876	1951
26 West Suffolk	Eriswell, Lord's Well Field	Native / Reinforced/Extant	1878	2021
26 West Suffolk	Thetford Heath	Native / Re-introduction / Extant	1878	2021
28 West Norfolk	Santon Warren	Native / Extinct	1880	1887
26 West Suffolk	Rushford Heath	Native / Extinct	1880	1905
26 West Suffolk	Barningham	Native / Extinct	1883	1883
26 West Suffolk	Brandon	Native / Extinct	1883	1883
28 West Norfolk	Croxton	Native / Extinct	1889	1889
26 West Suffolk	Wangford Warren	Native / Extinct	1889	1907
26 West Suffolk	Higham	Native / Extinct	1912	1912
26 West Suffolk	Barton Mills	Native / Extinct	1934	1934
26 West Suffolk	Eriswell - Icklingham crossroads, A11	Native / Extinct	1934	1958

Vice-County	Site	Status	Year of first record	Year of last record
26 West Suffolk	Eriswell Low arable	Native / Extinct	1939	1961
26 West Suffolk	Foxhole Heath South	Native / Extinct	1950	1961
28 West Norfolk	Weeting	Native / Extinct	1951	1964
26 West Suffolk	How Hill Track	Native / Re-introduction / Extant?	1951	2009
26 West Suffolk	Eriswell, Track to old chalk pit	Native / Extinct	1956	1956
26 West Suffolk	Mildenhall, High Lodge	Native / Extinct	1957	1961
28 West Norfolk	Brettenham, Langmere Hill	Native / Extinct	1961	1961
26 West Suffolk	Eriswell Low Warren inc SSSI	Reinforced / Extant	1961	2020
28 West Norfolk	East Wretham Heath	Introduction / Extinct	1962	1966
26 West Suffolk	Lakenheath Warren	Introduction / Extant	1964	2020
26 West Suffolk	Lakenheath, USAF Base	Native / Extant	1980	2020
26 West Suffolk	Elveden, Center Parcs	Introduction / Extinct	1991	1999
28 West Norfolk	Santon Track	Introduction / Extant	1996	2020
26 West Suffolk	West Stow Country Park	Introduction / Extinct	1997	1980
26 West Suffolk	Barton Mills, Mildenhall Woods, Three Hills	Introduction / Extinct	1998	2005
26 West Suffolk	Icklingham, Deadman's Grave	Introduction / Extant	1999	2020
28 West Norfolk	Santon Heath	Introduction/Extant	2020	2021

Status over time is presented in **Figure 1** and shows by decade, the number of native sites at which prostrate perennial knawel has been recorded in Breckland. ‘New sites’ are those where prostrate perennial knawel was recorded for the first time in that decade; ‘current sites’ are for those sites at which it was previously recorded and has been recorded again in

the same decade, 'former sites' are those where it was previously found but has not been recorded in the specified decade *or since.* The 'former sites' total is cumulative, and to reiterate, the table *excludes all translocations*.

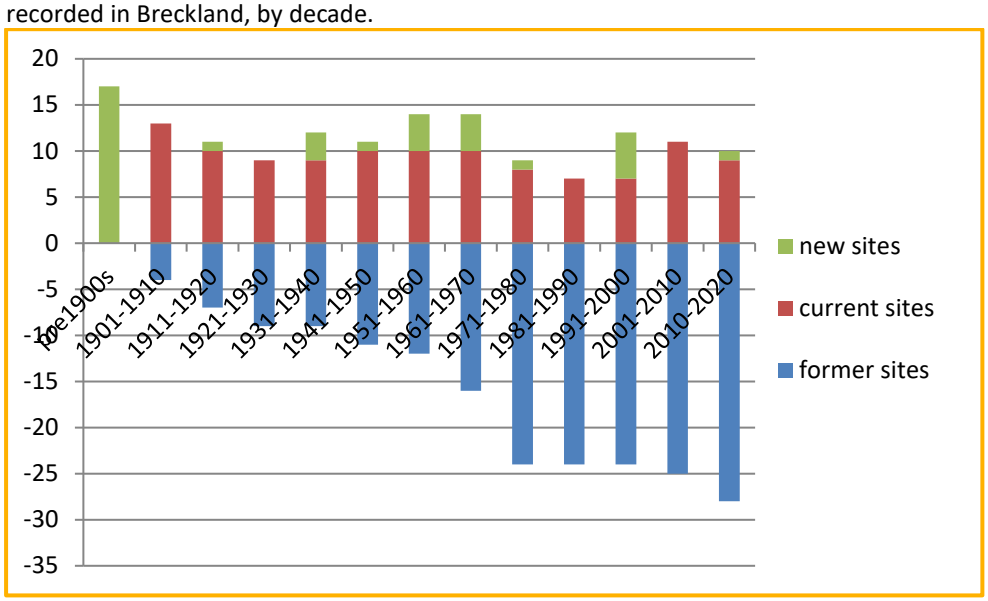
Figure 1. The number of native sites at which prostrate perennial knawel has been recorded in Breckland, by decade.



The figure shows that there is significant flux in the number of sites, with the plant appearing and disappearing with some frequency. This pattern of distribution follows the 'winking metapopulation' model, whereby the plant is adapted for transience, occurring sporadically at sites when they are suitable but disappearing when they become unsuitable and then recolonising when suitable again. This model requires there to be dynamic propagule transport between sites, so that recolonisation can occur when sites become suitable.

After 1970, however, the number of current sites declines to just four by 2020. Comparison with **Figure 2** however, which includes translocations shows that, since 1990, conservation work has held up the number of sites with 10 current populations, although losses have still occurred.

Figure 2. The number of sites, including translocations, at which prostrate perennial knawel has been recorded in Breckland, by decade.



3. Ecology and Life Cycle

3.1. Germination

The author's cultivated specimens produced seeds that germinated after rainfall irrespective of the time of year. Seedlings require open situations on well-drained sandy soils with a high percentage of bare ground (35%-50% appears to be optimal (Leonard, in Wigginton, 1999) where there is low competition from other species, whose development is inhibited in some way due to a particular factor, be it grazing, dryness, nutrient deficiency or simply time elapsing; such niches tend to be limited in extent or duration (Watt, 1971). The suitable conditions for germination are generated in a range of ways resulting from anthropogenic influences and natural processes, and are associated with features including open close-cropped swards, rabbit scrapes, and burrow entrances, mole-hills, poaching by livestock, vehicle movement and cultivation operations. Farther afield research investigating seed composition and vegetation gap colonisation in relation to burrowing activity and mound production by voles (*Microtus* sp.) in Pyrenean subalpine pastures demonstrated this type of disturbance increases short-term plant diversity and patch heterogeneity in graminoid – hemicryptophyte dominated pasture; ruderal species associated with the mounds, and otherwise scarce amongst dense pasture vegetation included Annual knawel and Wall speedwell *Veronica arvensis* (Gómez-García *et al*., 1999).

Watt (1971) records a soil pH of 4.9-6.8, which itself has led to an Ellenberg Reaction score of 4. However, as the range implies, the plant is tolerant of calcicolous conditions and, in the authors' view, tends to occur where bases have been leached out of calcareous sands. This would explain why the plant is only known from the Brecks and is in keeping with the fact that chalk and flint fragments can be found in association with it, even where the soil pH is low.

We can find no information about seed dormancy potential in Scleranthus perennis. However, Hoyle *et al* (2015) placed *Scleranthus biflorus*in a guild of immediately to rapidly germinating species; both *S. biflorus* and *S. uniflorus* are sold commercially and can come with the recommendation that they are stratified to break dormancy. We suspect that the latter is more successful when the seeds have been dried and leads me to the conclusion that the seeds probably do have some measure of dormancy potential. This would be a successful evolutionary strategy as seeds may be produced in periods of dry weather when it would be advantageous to delay germination until a wet period. Soil disturbance has been observed to stimulate germination (at Lakenheath RAF base in 2003) resulting in the production of many thousands of plants; while weather conditions undoubtedly played a part in this substantial response, it suggests that many seeds were lying in wait for a suitable event.

3.2. Development

In the right conditions (warm and damp, with no competition from other plants), seedlings rapidly develop into a prostrate herbaceous stem and start to branch. The plant is described a chamaephyte (a woody plant that bears its resting buds on or close to the ground) and, as it matures, the base becomes woody, and more stems appear. This activity is inhibited by the spread of grass species (Watt, 1971).

Plants are occasionally observed being buried by rabbit activity and windblown soil, and this has been considered detrimental to plant success, as has excessive disturbance by machinery or trampling from livestock. However, plants buried by windblown sand at Lakenheath Warren in 2020 grew rapidly, produced ascending stems that emerged from the sand and formed healthy mats of vegetation. They may in this way stabilise the sand somewhat and form an extensive root mat, resistant to blow out.

3.3. Flowering and Fruiting

Prostrate perennial knawel is described as flowering from June to September (Clapham *et al* 1987); however, Leonard (in Wigginton, 1999) observed anthesis at other times throughout the year and the authors have recorded flowering in most months. Detailed records have not been kept but flowers seem to appear with the advent of a dry spell following a damper period of vegetative growth. Svensson (1985) says numerous (c.20-500) small flowers are produced in dense terminal or axillary cymes, but the quantity of flowers will depend on the quantity of vegetative growth prior to the flowering episode. The flowers are more conspicuous than in Annual knawel and yield more nectar (produced in minute quantities by the disc (Svensson, 1985)) than those of Annual knawel and are visited by many small flies and automatically self-pollinated (Clapham *et al*. 1987). Svensson (1985) also observed that flowers were mainly visited by ants (*Formica (S.) rufibarbis* F., but several other species also. Note: According to the Bees Ants and Wasps Recording Society (BWARS) website (page updated 2002), F. rufibarbis is rare in Britain with substantiated records from Surrey and the Isles of Scilly, so not within the range of Prostrate perennial knawel. It nests on south facing banks with sparse vegetation on dry heathland, but some nests occur in Molinia/Agrostis swards. The species requires hotspots for success and in the lab survives desiccation better than most British ant species). Less frequent visitors included ladybirds (Coccinellidae) and Hymenoptera, indicating that out-breeding probably also occurs to some extent. Flowers are

protandrous with anther dehiscence taking place shortly after the bud opens, stigmas become receptive once the styles have elongated some 1-3 days after bud opening; after several days the stamens bend over towards the stigmas and self-fertilization is affected (Svensson, 1985). Ants visiting flowers hang over the corolla edge waving their antennae prior to entering the flower, and then penetrate the ring of anthers in order to reach the nectar producing disc; the amount of pollen adhering to a single ant varies and reflects differing routes taken by any one individual when entering the flower, pollen grains mainly attach to the head and antennae although some are subsequently removed either as a result of grooming or lost when the ant is moving between flowers (Svensson, 1985).

The fruit is an indehiscent one-seeded nutlet, usually 2-3mm, enclosed by the hardened wall of the perigynous zone and the persistent sepals, which are shed with it; the seed is lenticular and smooth (Clapham *et al*. 1987).

Watt (1971) puts forward 'human agency' as the likely means through which species of trackways are dispersed, citing the discernible spread of *Crassula tillaea* during the war period (assume WWII) in response due to increased levels of use, and highlighted the high co-incidence of *Apera interrupta*, *Herniaria glabra* and *Scleranthus perennis* records from or near to trackways. Historically cultivation practices would have served a similar function for *S. perennis* populations found in arable or fallow situations. Dispersal by means of windblown sand and/or soil is equally feasible as part of a mobile, dynamic system once commonplace in Breckland.

The perigynous tube is hairy and consequently there is potential for fruits to be transported by small mammals (rabbits etc), at least over short distances; the hairs are not noticeably barbed and therefore unlikely to adhere securely to a pelt for long periods suggesting their dispersal by this means over a wider area is doubtful.

3.4. Perennation

Despite its name, prostrate **perennial** knawel *Scleranthus **perennis** prostratus* does not reliably perennate. Leonard (2006) describes the plant as a biennial to short-lived perennial, and that tallies with our observations of cultivated plants. One of the authors grew mature 48 plants translocated in July 2019 from a naturalised (i.e., not wild) population. All survived till the following winter. Table 3 shows their survivorship. Plants believed to be new were delicately excavated and examined before replanting, to check that they were not attached to older stems or roots.

Table 3. Survivorship of 48 cultivated *S. perennis prostratus*

	7/2019	7/2020	10/2020	7/2021
Planted	48			
Existing		13	26	6
New		18		2
Died		35	5	18
Total alive		31	26	8

These few observations suggest that death rates are high but that recruitment from seed is important. In the right conditions, the plant can function as an annual (as Table 3 suggests) but is more commonly biennial, with some perennation into a third year. Our observations don't confirm or refute that further perennation occurs. This is because plants that die may be replaced by self-sown plants in their own pots, which is difficult to detect.

The words 'biennial' and 'perennial' are perhaps not appropriate for this species. They don't seem to be very seasonal but more weather dependent. Plants die back and become undetectable in drought periods; they may die or grow back when re-wetted. Return of damp conditions stimulates germination and plants grow continuously when it is warm and damp, flowering stems dying off after seeding but new ones being produced from the base. Annual functioning can occur when plants germinate in spring and then grow, flower, and set seed before dying off in the summer heat.

4. Habitat Requirements

4.1. The Landscape Perspective

Prostrate perennial knawel requires a dynamic environment. In the past, mobile sand-dune systems, wild grazers, and browsers, burrowing animals and the activities of stock would together have provided with open vegetation communities linked by transport processes, needed to maintain the metapopulation dynamics of Perennial Knawel. In more recent times, agricultural systems and commoning activities maintained suitable habitat conditions on an extensive scale across the Breckland landscape; irregular cultivation cycles for hay and crops, fallowing, livestock grazing and movement, excavation of materials and a network of inter-connected routes combining to mimic the more natural dynamics that they replaced. Examining the discontinuous distributions of some species found in open habitats, Pigott and Walters (1954), point out the Breckland habitats for *Scleranthus* are not natural ones, and that the present-day distribution in Breckland demonstrates this species' ability to profit from human activity.

However, the cessation of practices such as warrening, cultivation, extensive and long-term fallowing, long- and even short-distance droving, and their allied operations, has almost certainly led to the decline of *Scleranthus*, as well as a host other notable Breckland plants. The first report of the Breckland Biodiversity Audit (Dolman *et al* 2010) identifies a series of recommendations for dry terrestrial habitats; those considered pertinent to conservation of prostrate perennial knawel are listed below:

- Large numbers of priority species require heavy and intense grazing, this should be implemented across large parts of most heathland sites
- Physical disturbance should be applied to a substantial part of all terrestrial sites to provide conditions required by large numbers of priority species
- Heterogeneity, with areas of lighter grazing, structurally diverse swards, and juxtaposition with ungrazed elements (including ploughed or cultivated ungrazed margins within or alongside heath sites) all provide for additional species assemblages.
- Management should not be approached with the hope of keeping things from changing, rather management should be dynamic, episodic, and disruptive as gradual recovery from grazing or disturbance provides conditions and structures not found on homogenously managed sites

- Important assemblages that require physically disturbed *ungrazed* vegetation, including bare ground and ruderal plant communities, are best supported on arable field margins, through cultivated margin prescriptions, in the forest landscape, along lightly grazed margins of large, grazed heathlands, or in brown-field sites.
- Large, lightly grazed, heathlands provide opportunities for re-creation of breck arable and ruderal habitats through mechanical disturbance and cultivation

Conservation activity should seek to further efforts for the establishment of a dynamic network of habitats (and/or sites) comprising micro-topographical niches and active processes; these generate the full spectrum of successional stages to facilitate the spread of these species throughout the landscape.

4.1.1. Physical requirements

Soil samples were taken from all sites with extant native and introduced populations and from sites to which plants were translocated during this project. Prompted by this, USAF environmental staff arranged from soil samples to be taken from 15 sites across RAF Lakenheath air base both from where prostrate perennial knawel grows and from where it is not present. Results have not yet been received for these samples. As the air base has the largest native population of this species these results are key to interpreting results from the other sites. Analysis of these results and the understanding they will provide about the physical requirements of this species will be an important contribution to the legacy of this project.

4.2. Communities and Vegetation

Prostrate perennial knawel was described by Bennett ((1914) in Watt, 1971) from localities that displayed no evidence of past cultivation and 'near Lakenheath it grows on a heath with *Medicago sylvestris* (now *M. falcata*), *M. minima*, *Silene otites* etc. which certainly has never been broken up'.

Watt's own extensive observations (all 1971, unless otherwise specified) refer to 'its occurrence on three fallows, three trackways and one area which looks natural but is reported to have been cultivated in or just after the First World War and is probably the area referred to by Bennett'. Watt continues, recounting 'the soil is variable: the higher terrain carries calcicoles, the lower has an acid soil (pH 5.7) with numerous flints on the surface and carries a community which includes the following species: *Agrostis canina*, *Aira praecox*, *Filago minima*, *Hypochaeris glabra*, *H. radicata*, *Jasione montana*, *Ornithopus perpusillus*, *Teesdalia nudicaulis* and *Trifolium arvense*'.

Summarising, Watt concluded prostrate perennial knawel is present in a community where the components are 'socially equal' and the competitive ability of associates that would typically suppress *Scleranthus* in a Mesobrometum grassland (Grassland B – Breckland variant of calcareous grassland [NVC: CG7b]) are restricted in some way by inorganic factors or merely time. He divided the Breckland rarities into three guilds based on their stature, life cycle and competitiveness, placing *Scleranthus* within a group containing species that are small in stature, predominantly annual, and associated with either arable and fallow fields or bare areas found amongst natural vegetation (including those present amongst short open turf where suitable soil conditions are available). Species in the guild are: *Apera interrupta*,

Crassula tillaea, *Galium parisiense* ssp. *anglicum*, *Herniaria glabra*, *Medicago minima*, *Scleranthus perennis* ssp. *prostratus*, *Silene conica*, *Thymus serpyllum* ssp. *serpyllum*, *Veronica praecox*, *V. triphyllos* and *V. verna*.

He observes that *'The situation may be compared with that on stable dunes where there are several annuals (including locally Silene conica and Medicago minima) in an open turf. As Willis (1963) has pointed out the factor inhibiting the dominance of species capable of suppressing the small annuals may be a shortage of appropriate nutrients. At the present time in Breckland this particular assemblage of species is rare'.*

The soil on the shallow highly calcareous soils of the Xerobrometum appear to be a limiting factor for the establishment of some species including prostrate perennial knawel, where attempts by Watt to establish this species failed (Watt, 1971). Prostrate perennial knawel has been recorded in the past at Barnhamcross Common (now extinct but recently reintroduced), where soils are variable (highly calcareous - sandy) and have a pH range of 5.0-7.0. Watt draws attention to both the geographical position (close to Thetford) and common land status as a limiting factor in respect of rabbit numbers, whilst also highlighting human disturbance associated with commoning activities; here prostrate perennial knawel was noted growing on a trackway amongst open *Carex arenaria* in an area known to have never been a warren, nor presumed to have been in cultivation.

In the National Vegetation Classification (NVC: Rodwell 1991), *Scleranthus perennis* is associated with U1 *Festuca ovina-Agrostis capillaris-Rumex acetosella* grassland, Typical sub-community. In this vegetation type perennials are usually low in cover and many stands have a rather coarse weedy look, while some contain small amounts of *Calluna vulgaris*, *Pteridium aquilinum* or *Carex arenaria*; the data available shows *Scleranthus perennis* is recorded from these poorer swards. Other notable Breckland species found in this situation include *Silene conica* and *S. otites.* [N.B. *Scleranthus perennis* is not listed in any OV communities, while *S. annua* is found in OV1 and OV5; former arable localities would most likely approach OV3.]

The chief botanical interest of the Brecks, however, centres on the guild of species that mainly belong to the steppe element (Salisbury 1932) but including a few others outside this group. Collectively they range on the continent from Scandinavia to the Mediterranean and eastwards to Russia and Siberia. In UK they are either confined, or nearly so, to the Brecks (*Scleranthus perennis* subsp. *prostratus* (Sell 1963), *Thymus serpyllum* subsp. serpyllum (Pigott 1955), *Veronica spicata* subsp. *spicata*) or are (or were) more common there than elsewhere (Watt, 1971).

4.2.1. Continental affinities

Watt's ungrazed and grazed grassland B type vegetations are readily assigned to the Brometalia of the class Festuco-Brometea, and the few examples with *Scleranthus perennis, Thymus serpyllum* and *Veronica verna* to the Corynephoretalia in the Sedo-Scleranthetea. On phytogeographic and ecological grounds, Scandinavian work supports this separation of communities for the continent (Albertson (1950) and Konigsson (1968) for the Alvar of Oland, Sterner (1922) for South Sweden, Bocher, Christiansen & Christiansen (1946) for North Jutland). More specifically Andersson (1950) distinguishes (in 'Scanian sand vegetation') acidic grass-heath (Corynephoretum) from 'basic grass-heath' with two communities, the Koelerietum and the Avenetum. The list of species characteristic of the

Corynephoretum includes many annuals (*Aira caryophyllea, A, praecox, Filago minima, Hypochaeris glabra, Ornithopus perpusillus* and *Teesdalia nudicaulis*) as well as the perennials *Corynephorus canescens, Jasione montana* and *Scleranthus perennis*. For the maintenance of their characteristic floristic composition, the Koelerietum and the Avenetum depend on grazing: between them they include *Alyssum alyssoides, Artemisia campestris, Carex ericetorum, Corynephorus canescens, Holosteum umbellatum, Hypochaeris maculata, Medicago falcata, M. minima, Phleum phleoides, Veronica spicata* and *V. verna.* The Koelerietum is in a warmer and drier habitat with a higher percentage of annuals and smaller plants than in the Avenetum, whose soil contains more 'mo' (silt). Competition doubtless plays an exclusive part (All Watt, 1971).

Pigott & Walters (1954) note however that 'disturbed soils with more open communities in any case favour the persistence and local spread of these species, and that the significance of early human settlement of the chalk was considerable, not only for the consequent forest destruction, but also, of much greater importance, through the creation of impermanent ruderal-type communities in or around which these species of low competitive power could spread. The 'continental' rarities of the Breckland are particularly interesting in this connexion. They can be divided into two general types; the annual weeds, many of which occur, either largely or in some cases exclusively, in arable and disturbed land (e.g., *Veronica triphyllos, V. praecox, V. verna, Apera interrupta*, etc.), and the perennials (and a few annuals), to which it is possible to assign a semi- natural or natural habitat in the grassland A and B types (cf. Watt, 1940). Even in the second group, however, some species take advantage of the open communities at the margin of arable land (e.g., *Scleranthus perennis, Artemisia campestris, Medicago falcata,* etc.), and some even occur among crops (e.g., *Muscari racemosum* (now *M. neglectum*)

4.3. Summary of Habitat Requirements

Habitat features important to prostrate perennial knawel are summarised below in **Table 4**.

Table 4: Habitat features important to prostrate perennial knawel in Britain.

TYPE	DESCRIPTION
Physical & topographical	A lowland species of dry, acidic sandy soils. Sites are in +/- level, open situations with little shade. Low rainfall, high summer temperatures and cold dry winters.
Vegetation/structural	A poor competitor characteristically reliant upon the regular provision of open disturbed ground or maintenance of short, close cropped swards containing patches of broken turf / exposed soil for germination and plant establishment. Associated with the **U1** NVC community (and perhaps formerly OV3 but does not feature in published accounts) where competition from graminoids and perennial forbs is suppressed to varying degrees by management, climate, and nutrient poverty.

TYPE	DESCRIPTION
Processes	Exposed soil is required for germination, plant development and seed production, disturbance is provided by a variety of means including grazing, localized quarrying, rabbit activity, mole-hills, poaching by livestock, vehicle movement on trackways and agricultural operations for arable situations. Seed dispersal linked to equipment, vehicle, and livestock and wild animal movements.
Chemical	*S. perennis* is associated with nutrient poor acidic soils; but with some calcium carbonate present at low levels i.e., probably leached out. In agricultural situations the application of fertilisers and herbicides poses a threat, and the influence of these operations may extend to plants found on neighbouring features e.g., trackways.

5. Management Implications

The decline and loss of natural dune geomorphology underpins the decline of prostrate perennial knawel, but this is coupled to the decline of traditional extensive land use practices. The principal implication of this is that management is required to simulate those natural and semi-natural conditions.

Where plants survive, active management processes must be maintained, and combined with measures to routinely generate open ground to allow for germination events. Creating patches of disturbed soil can be readily incorporated into site management prescriptions and should aim to provide suitable conditions for recruitment on a rotational basis both within existing stands and beyond; disturbance can be achieved using machinery e.g., rotovation, ploughing or turf-paring, or manually at a smaller scale. Each of these approaches generates a different substrate and has its own implications for the plants (e.g., turf-paring can remove existing populations but is a very useful approach for preparing ground for introductions.

The movement of livestock and vehicles along trackways can produce the desired effect and offer potential for dispersal and establishment of new colonies, provided that the type and frequency of use disturbs and loosens soil rather than compacting it.

In grassland sites, grazing by domestic livestock and wild animals helps to maintain a short sward and can break up turf through poaching, scrapes, burrowing etc, but can also encourage a tight sward; installing features such as blind fence runs and single fence posts encourages greater levels of wear to counter this, as animals preferentially walk or lounge against them. Where it is not possible to graze, the alternative is to mow; observations post 2000 at RAF Lakenheath have highlighted the benefits of cutting the vegetation very close to the ground but where rabbit numbers are low, periodic scarification or harrowing will likely be needed to generate bare ground.

The lack of seasonality in the life cycle of prostrate perennial knawel means there are few timing issues with management but, where populations are small and isolated, it is best to avoid applying management if the population is dominated by newly germinated plants. Management should be delayed until after a fruiting phase, although this requires flexibility by the manager and frequent checking of the condition of plants.

6. Threats, and factors leading to loss or decline or limiting recovery

Prostrate perennial knawel requires processes that generate open disturbed soils for germination and establishment. These processes, be they natural or anthropogenic, have diminished as traditional land use such as warrening and agricultural practices have shifted in the twentieth and current century. The myxomatosis epidemic in the 1950's and large-scale afforestation since the 1940's has had a profound influence on Breckland the effects of which continue today.

The absence of active disturbance processes leads to increased vegetation density and the out-competition of prostrate perennial knawel.

Table 5: Threats to the survival of prostrate perennial knawel in Britain.

TYPE	THREAT
Habitat destruction	Agricultural intensification. Afforestation. Built development. Absence of processes to produce bare soil conditions. Nitrogen pollution.
Successional	Succession to dense grassland swards, scrub communities where plants then are outcompeted. Density of bryophyte cover can impact on/have a detrimental effect on seedling/plant performance.

7. Conservation and Monitoring

7.1 Conservation

Prostrate perennial knawel is listed under Schedule 8 of Part I of the Wildlife and Countryside Act, 1981 (as amended).

Extant populations (native and introduced) of prostrate perennial knawel receive protection at a site level through designation as a Site of Special Scientific Interest (SSSI's) or inclusion within a county wide Local Sites System as listed in **Table 6**.

Table 6. Protection for sites with extant populations of prostrate perennial knawel (SSSI: Site of Special Scientific Interest; SPA: Special Protection Area (for birds); SAC: Special Area of Conservation.)

SITE	DESIGNATION
Barnhamcross Common	SSSI, SAC, SPA, LNR
Eriswell Low Warren	SSSI, SPA
How Hill Track	SSSI, SPA
Icklingham, Deadman's Grave	SSSI, SAC, SPA
Lakenheath Warren	SSSI, SAC, SPA
Lordswell Field	SSSI
RAF Lakenheath	SSSI, SAC
Santon Track	SSSI, SPA
Santon Heath	SSSI, SPA
Thetford Heath	SSSI, SAC, SPA

7.1.1. Current Conservation Schemes

Environmental Stewardship: This agri-environment scheme is the primary conservation programme available to landowners and managers in England and provides funding to deliver effective environmental management on their land; the scheme contains four elements three of which are relevant to Breckland. The scheme is administered by Natural England.

- Entry Level Stewardship (ELS)
- Organic Entry Level Stewardship (OELS)
- Higher Level Stewardship (HLS)

The plant was a target species within the National Lottery Heritage Funded Shifting Sands Project, a landscape scale conservation project aimed at conserving a range of species and solving some of the problems faced by Breckland wildlife. Under that project targeted management and selected translocations works were undertaken to enhance the status of the species. See Table 7 below.

Table 7	**Considered extant in 2018**	**Current/ former site**	**Habitat enhancement works**	**Translocation**	**Notes**
Eriswell Low Warren	Yes	Current	Turf-paring	No	
Lordswell Field, Eriswell	No	Current	Turf-paring	Reintroduction 2019	Native plants were found on site immediately after reintroduction works so, in effect, a reinforcement.

Deadman's Grave, Icklingham	Yes	Current	Ploughing		
Lakenheath Warren, Lakenheath	No	Former	Turf-paring	Reintroduction 2019	A former, failed, introduction site
How Hill Track, Eriswell	Yes	Current	Turf-paring	No	
Santon Heath, Lynford	No	No	Turf-paring	Introduction 2019	
Barnhamcross Common, Thetford	No	Former		Reintroduction 2020	…into areas prepared under an earlier project

It is too early to say whether these recent efforts have been successful.

7.1.2. Former conservation activity

Prompted by concern that a known prostrate perennial knawel site may be under threat, A.S. Watt carried out one of the earliest recorded introductions of this species at East Wretham Heath in 1962. Seeds were sown in an area of comparable habitat, containing a limited flora, open vegetation cover estimated at 50% and some small chalk fragments present on the surface resulting from rabbit activity. Associate species listed included *Agrostis canina, A. tenuis, Festuca ovina, Rumex acetosella* and *Polytrichum piliferum*. Seed were sown in two 1m² plots and by 1969 a total of thirteen plants had established across both plots. A count of 28 seedlings was made from one plot in May 1970, and the majority of these survived the ensuing severe drought (Watt, 1971). No further details have been traced.

Subsequently, a series of introductions were carried out at 10 sites in Breckland since the early 1960's (Table 8). Overall, attempts to (re)introduce *Scleranthus* have met with mixed fortunes; techniques employed to establish the preferred open, disturbed conditions include ploughing, rotovating strips and turf-cutting. Fluctuation in rabbit numbers, levels of mole-activity and grazing intensity and in some cases human pressure all influence habitat suitability to varying extent depending upon circumstances and timings e.g., in the case of grazing, probably exacerbated by inaccurate assumptions of what the appropriate habitat should look like (such perceptions are probably largely based on sites where populations are declining or have dwindled away completely). Periodically this has resulted in the need for further intervention using mechanical or manual means to reduce competition and maintain niches for seedling establishment. Conversely high levels of disturbance of any type or origin are detrimental to plant performance particularly at the seedling stage. An example of this is provided by the introductions at Three Hills, Mildenhall, one along a forest ride, the second on recently restored heathland. The former was lost when, with the restoration of a section of forest to heathland, the track became a dead end and so walkers and vehicles stopped using it; the second was lost when plants were trampled after water for grazing animals – required to get the heathland into good condition - was located adjacent to the introduction site.

Table 8. Summary details for sites in Breckland where prostrate perennial knawel has been (re)introduced before 2018.

Site	First record pre-introduction	Last record post-introduction	Peak count pre introduction	Year(s) (Re-) introduced	No. of plants introduced	Last record	Peak count post introduction	Considered Extant (2021)
Three Hills, Barton Mills / Mildenhall Woods (ride)				**1998**	60			
				2000	14			
				2003	9	2003	41	No
Three Hills, Barton Mills (heath)				**2005**	28	2005	0 – lost, all trampled	No
Center Parcs, Elveden	1991	1991	25	**1998**	3	2001	?	No
				2001	5		?	
East Wretham Heath				**1962**	seed	1970		No
Deadman's Grave, Icklingham				**1999**	?	2020	240	Yes
				2004	27		6	
				2006	14		106	
How Hill Track, Eriswell	1951	2001	100+	**2002**	39		24	Yes
				2004	17		140	
Lakenheath Warren, Lakenheath				**1964**	?	1983	6	No
Santon Track, Lynford				**1996**	?	2021	844	Yes
Thetford Heath				**1963**	?	2000	?	Yes
				1970	?		?	
				1980	8 plants, 3150 seeds		263	
				1996	?	2021	1327	

West Stow Country Park				**1980's**	?	1997		No
				1997	16			

7.2. Monitoring and the Common Monitoring Standard

Individual flowering plants are relatively easy to recognize, and counts should be made for all populations where plants number <1000. Above this figure it may be necessary to calculate the area occupied and estimate the number of plants present. Surveys should be made during the peak flowering period from June to November, recognising that the plant has growth patterns that follow the weather rather than the seasons.

Counting this plant can be problematic, however. It can be difficult to distinguish between more than one plant, or one plant which has been partly buried by sand with branches emerging that look like a second plant. It can form a mat when growing vigorously and there may be numerous seedlings appearing beneath the mat. Similarly, vigorous neighbouring plants may join to form a single mat. Numerous seedlings may appear beneath the mat. Identifying distinct individuals is therefore difficult. While it is important to try and get an accurate count, including seedlings, there are clearly limits to the practicability of this, and to the patience and diligence of any recorder. Estimates of number should be accompanied by the method of estimation and a narrative account describing the situation, to enable comparisons to be made between sites and over time.

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BRPD = Breckland Rare Plant Database. Held by Plantlife

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10. Links

ARKive species web page for ***Scleranthus perennis* ssp. *prostratus***
http://www.arkive.org/perennial-knawel/scleranthus-perennis-prostratus/

Appendix I. Site Register

History of records at individual key sites

1. **Elveden area**

   There are records of prostrate perennial knawel from Elveden from 1677 to 1910. In 1816 the location is given as 'in sandy cornfields around Elveden', while in 1848 and 1878 the location is 'around Redneck Farm'.

2. **Culford**
   Prrostrate perennial knawel was recorded here in 1774, 1804 and 1883, but not since.

3. **Mildenhall area**

   Prostrate perennial knawel was recorded here from 1827, with regular records up to 1913, the last being in 1934.

4. **Mildenhall, near St Helena Cottages**

   Prostrate perennial knawel was found here between 1827-1892 on sandy heaths/warrens, and again between 1906 and 1913. It was found again in 1949, 1953, with the last record in 1974.

5. **Icklingham Plains**

   Prostrate perennial knawel was found here from 1828 and then through the 1800s, and then in 1910, 1939 and 1953. It was not found in 1975, nor since.

6. **Icklingham, Rampart Field Area**

   Prostrate perennial knawel was first found here in the 1770s and then regularly through the 1800s. It was last recorded here in 1912, and not located in 1976.

7. **Deadman's Grave, Icklingham**

   Prostrate perennial knawel was first introduced to this site in 1999 and then again in 2004 and 2006. The area was chosen at the southern end of the site where the ground had been ploughed in preparation. This management has been repeated intermittently, including in 2018. 11 plants were found in 2020 but survey returns are greatly affected by weather conditions and such a number may not reflect the real status of the plant here.

8. **Eriswell area**

   Prostrate perennial knawel was first recorded here in 1846, found in 'sandy fields about Eriswell'. 'Enormous plants' were found in 1889, and in 1939 and 1949 plants were found in open sand, but not found in 1950 when the area had been ploughed.

9. **Lordswell Field, Eriswell**

   The plant was first recorded at precisely this site in 1954, although known from the area for decades before then. Post 1954, the plant was recorded fairly regularly at his location, with in

excess of 1000 plants seen in 1974, but regular monitoring seems to have been coincided with a decline in eth condition of the site, numbers oscillating between none and 300 up until 2013 when again none were seen. The plant was believed to have gone extinct there, as it was not recorded since 2012, and in 2019 15 plants were reintroduced into areas which had been turf-pared in preparation. As luck would have it, immediately after the reintroduction work was completed, several native specimens of prostrate perennial knawel were located a short distance from the translocation. Further plants were located in 2020.

10. **Thetford Heath**

Prostrate perennial knawel was recorded here from 1878 to the end of the 19th century, again in 1919-1922, 1934 and 1950. In 1975 it was recorded as extinct. In 1963, it was introduced to Site 1, and again in 1980 when 8 plants and approx. 3150 seeds were used. The main site had been ploughed and divided in to 11 strips for different managements: one strip had received growing plants, the others seed. One strip was a control, one rotovated every third September, one rotovated every September. In an additional area three plants were put in a rabbit exclosure. In 1983 there were 90+ plants in the main area, none in the additional area. By 1992 this had increased to 263 plants. In 1996 there was a further introduction at a new area of the heath: Site 2.

Visits to Site 1 were limited by the presence of Stone Curlews and Prostrate perennial knawel was not located here in 2004 and 2005 when visits were possible. It was noted that the strip was vegetated over and heather invading, but it was well rabbit grazed. Good numbers however were counted at Site 2 up to 2009, when 1327+ plants were recorded. Numbers have since dwindled somewhat but the plant was still extant in 2020 when 19 plants were recorded; this might seem dangerously low, but survey returns are greatly affected by weather conditions and such a number may not reflect the real status of the plant here.

11. **Barnhamcross Common**

First recorded here in 1738, prostrate perennial knawel was regularly recorded here until 1961. There are few notes about its location; in 1925 it was found on ‘banks and tracks where competition from Furze is less keen’ and in 1961 it was ‘near recently bare bits (rabbits) and where pressed down by vehicles’. It was last seen here in 1971, it was not located in 1974.

A reintroduction of 20 plants was made in June 2020, in two plots close to each other. At the time of writing, it is too early to say whether this has been successful.

12. **Eriswell-Icklingham crossroads, A11**

Prostrate perennial knawel was found here in the 1930 and 1950s, with the first location at a field margin at the crossroads. The last record was in 1962. The site had been destroyed by 1974, when the new crossroads were built.

13. **How Hill Track, Eriswell**

Prostrate perennial knawel was first recorded here in 1951, then regularly until the mid-1970s, with a peak count of 100+ in 1969. Plants were found in sandy places and, for example, in 1974, the 15 recorded plants were found mostly on bare soil in the centre of the track. The site was damaged by the wet winter/spring of 1975, heavy farm machinery and cattle trampling, and only two plants were found; the species was then not located in 1976-1980. In 1981-1983 there was

some recovery, with 4-17 plants counted in dry, dusty soil. Prostrate perennial knawel was again not located 1989-1993, with the track overgrown and stabilised. In 1992 the track was disturbed using a 'shakerator' and in 1993 large clods were shaken and removed. In 1994, two plants were found in the exact location they were found in 1983. Numbers of plants again increased, with a peak of 101 plants in 1998. In 1999, 47 plants were counted, the track had less than 5% bare ground and lots of shredded newspaper covered plants. More disturbance was suggested in addition to the September swiping and forage harvesting (no date is given for when this latter management started) and the possibility of an uncropped strip in the adjacent field. In 2002 the track was in good condition; 38 plants were counted, and 2 flowering plants and 37 vegetative plants were put along the 35m strip to bulk up the populations. In 2004, a further 17 flowering plants were put on the track. In 2005, 17 plants and 123 seedlings were counted, the track was very rank and dense, and the minute seedlings were located under the dead parent plants. Prostrate perennial knawel was not located in 2006 and 2007, with the centre of the track too vegetated and nettle invading. In 2008 and 2009, 3 and 5 plants were counted, in 2009 the track and bank adjacent to the field was swiped and a new arable headland created. The plant has not been seen here since but may still be present in the seed bank. The turf was pared off track in 2019 to improve habitat conditions.

14. **Eriswell Low Warren inc SSSI**

    Prostrate perennial knawel was first recorded here in 1971 along the sides of a worn cattle track. This site has been extensively studied and divided into sub-sections for records and counts of prostrate perennial knawel . The Breck Rare Plant Database should be consulted for the detail of the history of prostrate perennial knawel at this site. In the late 1970 there were peak counts of 1670 plants with presence in the majority of sub-sites. In 1979 one of the best sub-sites was ploughed in error. By 1986 the count totalled only c200 plants and 7 of the 13 sub-plots had no records, probably as the result of dense vegetation; the sub-site with most plants had open vegetation and rabbit activity. Through the 1990s management was undertaken to support this species including ploughing of furrows and a new area rotovated and plants put in this new area (note: these are not described as Introductions). and sheep exclosures constructed. In 1999, 1190 plants were counted. From 2000-2009 there continued to be counts in the hundreds, with a peak of 3,000+ in 2007. In 2019, a further area of turf was stripped towards the north-east corner, close to existing plants.238 plants were recorded at the site in 2020.

15. **Eriswell Warren and Low Arable**

    Prostrate perennial knawel was first found here in 1939 and again in 1944 and 1961. It was not located in 1975.

16. **Lakenheath, RAF Lakenheath**

    Prostrate perennial knawel was first recorded here in 1980 and since has been found in large numbers, with 6 counts of over 1,000 plants up to 2007. The regular low cutting of the grass is thought to benefit the species. A significant part of one of the larger sub-populations was translocated in 2020 to make way for an electricity sub-station.

17. **Lakenheath Warren SSSI**
    Plants were introduced by A S Watt in 1964. A peak of 29 plants was reached in 1971 but the stand dwindled till it was last recorded in 1983. A new reintroduction was attempted in 209 at the same location after the ground was prepared by stripping the turf. It's too early to say whether that translocation has been successful.

18. **Santon track**

    Prostrate perennial knawel was introduced here in 1996 and there have been counts of 100+ plants here every year between 2001-2009, with a peak of 844 plants. In 2008, Friends of Thetford Forest carried out management, removing rank grass, heather seedlings and overhanging Oak branches. In 2009 it was noted that the path needs skimming/widening back to the state when the plants were introduced in 1996. This work was completed by FC and further scraping has taken place alongside the track, with limited success. In 2020 over 500 plants were recorded on the widened track, but not in the adjacent scraped areas.

19. **Santon Heath**

    Two sets of 10 plants were introduced here in December 2019, into ground that was previously prepared by stripping the turf off. At the time of writing, all plants were doing well and there was recruitment form seed, but it is still too early to say if the translocation is successful.

20. **Barton Mills, Mildenhall Woods, Three Hills**

    60 plants of Prostrate perennial knawel were introduced here in 1998. In 1999, 190 plants were counted, but were shrivelling and the track was dry, with less than 5% bare ground in most parts. In 2000, 185 plants were counted and a further 14 plants introduced. In 2001 this reduced to 41 plants, with lack of dog walkers because of foot and mouth restrictions keeping the sward open. In 2003 only 2 plants were found, and the track was now unsuitable and no longer used by dog walkers because of adjacent fencing for regeneration of heathland. 9 flowering plants were put on conservation ride 306. In 2004 no plants were located. In 2005, 28 small clumps of seedlings were introduced and marked with a stick. Later in the year no plants were found here, the area had been trampled by sheep, waste tanks for the animals had been put close by.

21. **East Wretham Heath**

    An introduction was attempted in 1962, using seed. It seemed hugely successful for a brief period but dwindled quickly and plants were last seen in 1966.