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Cover: *Gentianella campestris* in its natural habitat, i.e. nutrient poor semi-natural grassland.
Photo by Lena Johansson

Summary

28 populations of the endangered biennial herb *Gentianella campestris*, in the county of Södermanland in Sweden, which have been censused since 1993, were re-visited to assess the population dynamics and extinction rates in relation to grassland management, soil conditions and the configuration of the landscape. The populations have fluctuated significantly during the years 1993-2005, some extremely. 12 of the populations have had less than 50 individuals on average (median value) 1993-2005. 25% of the populations are presumed to be extinct, but only in two of them the management has ceased. Among the five populations with ceased management three still have subsisting populations. The population size in 2005 was correlated to the size in the years 1993-94 suggesting that the populations have the maintained their relative size during the period. The populations are isolated but population size was not related to habitat area. Among habitat qualities only tree coverage was related (negatively) to the population size. There was no relationship between soil conditions and population size. Surprisingly there was no clear effect of present management status, or previous management, on the population size and extinction in these populations. Ceased management is likely to lead to extinction of G. campestris populations, although it may take over a decade. Continued management is, however, not sufficient for maintaining the populations. The possibility that management regime still has an effect on population dynamics is discussed.

Sammanfattning

28 populationer av den utrotningshotade tvååriga örten fältgentiana (*Gentianella campestris*) i Södermanlands län i Sverige som räknats sedan 1993 återbesöktes för att uppskatta populationsdynamik och utdöendet i relation till hävd, markförhållanden och landskapets utseende. Populationerna har fluktuerat betydligt under åren 1993-2005, en del extremt. 12 av populationerna har haft mindre än 50 individer i genomsnitt (medianvärde) 1993-2005. 25 % av populationerna är förmodligen utdöda men bara i två av dem har hävden upphört. Bland de fem populationer som hävden upphört har tre fortfarande kvarvarande populationer. Populationsstorleken 2005 var korrelerad med storleken åren 1993-94 vilket antyder att populationerna har behållit sin relativa storlek. Populationerna är isolerade men populationsstorlek var inte associerad med habitatarea. Bland habitategenskaper var det bara trädtäckning som var relaterat (negativt) med populationsstorlek. Det fanns inget samband mellan markförhållanden och populationsstorlek. Förvånansvärt fanns det ingen direkt effekt av nuvarande hävdstatus, eller tidigare hävd, på populationsstorlek och utdöende i dessa populationer. Upphörande hävd leder med tiden till utdöende av fältgentianapopulationerna, även om det kan ta mer än 10 år. Vidmakthållen hävd är

dock inte tillräckligt för att säkra populationernas fortbestånd. Möjligheten att hävdregimen fortfarande har en effekt på populationsdynamik diskuteras.

Introduction

The semi-natural grasslands in Sweden have a long continuity of management that dates back to the beginning of the Iron Age, 2500 years ago, when use of permanent fields was introduced. The characteristic agricultural landscape with open pastures expanded and became more pronounced and the open grassland pastures and wooded meadows became vital as they supplied livestock with fodder, which in turn gave manure to the arable fields. This form of land use remained into the beginning of the 19th century when the agrarian revolution began. The use of the land changed with new agricultural implements and methods and also a land division law was introduced by which the character of the settlements changed (Riksantikvarieämbetet 1996). A major change was the introduction of ley production on arable fields, which replaced mowing on semi-natural meadows. The second major change in Sweden came when manure was replaced with artificial fertilizers during the period from the late 19th century to after the Second World War. The area-loss of semi-natural grasslands was enormous during this period (Riksantikvarieämbetet 1996). The long continuity of management by grazing and mowing of these unfertilized grassland pastures and meadows have created highly species-rich habitats and the remaining semi-natural grasslands species show a high diversity of plants, fungi and animals. Many of these species are endangered or vulnerable (Gärdenfors 2005).

This area loss of semi-natural grasslands has resulted in a fragmentation of the remaining sites. An increased isolation between fragments results in a decreased colonization rate and the longer distances between fragments makes dispersal difficult. Also the habitats areas have been reduced resulting in decreased population size of inhabiting species. The effects of fragmentation on the community level and on population dynamics are hard to generalize, as they probably are species and site specific (Eriksson & Ehrlén 2001). Effects of fragmentation on community level include a reduction of species richness (Lennartsson & Svensson 1996) and makes the plant communities more vulnerable to invasive generalists (Kiviniemi & Eriksson 2002), affect plant and animal interactions (Lennartsson 2002), change the seed dispersal by animals (Ekstam & Forshed, 2000). On the other hand, fragmentation may have positive effects on plants when herbivore and pathogen are unable to sustain populations in the fragmented landscape (Kéry et al. 2001). The effects on population dynamics when the population size decreases is an increased extinctions rate due to e.g. inbreeding and environmental and demographic stochasticity. The genetic and demographic effects on small populations can lead to erosion of genetic variation and reduced population viability (Fisher & Matthies 1998). Also the seed production and seedling recruitment is affected by fragmentation but are thought to be species specific. Other factors that can have effects on population dynamics are changed habitat quality, disturbance regimes, edge effects and competition

from other species. Sensitive species can be strongly affected by habitat changes (Lennartsson & Svensson 1996) like the change of management methods, for example the shift from mowing to grazing in the semi-natural grasslands (Lennartsson & Oostermeijer 2001). Also soil type at different depths may influence species richness, and the local relief or form on the sites may influence the species richness (Cousins & Eriksson 2002).

It is important to consider the time scale, not only the spatial dimension, of fragmentation as many species show a slow response to the landscape changes, with time lags up till a hundred years (Lindborg & Eriksson 2004; Eriksson & Ehrlén 2001). Many semi-natural grasslands still have a high species richness due to a long management history (Cousins & Eriksson 2001) and they may in the future show a slow decline in species richness.

Due to habitat loss and change in habitat quality of the semi-natural grasslands many of the grassland species have declined (Lennartsson & Svensson 1996). One of these endangered species is the biennial herb *Gentianella campestris* (L.) (Gentianaceae) growing in unfertilized grazed or mown semi-natural grassland. *G. campestris* germinates in the spring and forms a rosette the first summer and over-winters with a taproot with a terminating bud, the second summer it flowers and dies. Two seasonal ecotypes types are known, early and late flowering (Lennartsson & Svensson 1996). Some populations have an elongated flowering time and in the north of Sweden there is an intermediate type (Lennartsson 1996). The early type of *G. campestris* flowers from late June to mid July and the late type begin flowering early in August (Lennartsson 1996). This variation in flowering time is genetic and is little influenced by surrounding factors like habitat quality (Lennartsson 1997).

G. campestris is pollinated only by bumblebees (Lennartsson 2002) and has a temporary seed bank (Lennartsson & Svensson 1996) but thanks to self-pollination and high self-compatibility, 85-95% of the seed embryos produce seeds without pollinators (Lennartsson et al. 2000). Some populations have herkogamous flowers with spatially separated anthers and stigmas and this can reduce seed set in absence of pollinators (Lennartsson 2002).

G. campestris is avoided by animals because of bitter tasting glycoside compounds (Lennartsson et al. 1998). However, with a hard grazing pressure it can be damaged and is then known to overcompensate (Lennartsson et al. 1997). The damage can result in an enhanced fruit and seed set if the damage is induced at the right time (Lennartsson et al. 1998) but also the amount of damage affects the resulting compensation (Huhta et al. 2000).

The last 50 years *G. campestris* have disappeared from 90% of its localities in central Sweden (Lennartsson & Svensson 1996). Since the species is associated with semi-natural grassland with high diversity and high species richness it could be used as an indicator species for evaluation of conservation options and management regimes for the still remaining grasslands.

In 1993 the Department of Botany at Stockholm University started a research project on semi-natural grassland and did an inventory of 28 sites with *G. campestris* in the county of Södermanland. The selection of these 28 sites was based on the pasture and semi-natural grassland inventory (Rydberg & Vik 1992) made in the late 1980's. These populations have been followed with varied extent until 2003 and the data has previously only been analyzed with regard to synchronization of the population dynamics (Eriksson & Ehrlén, 2001).

The aim of this study was to re-inventory the 28 populations and investigate the connection between population dynamics, population extinction, the maintenance of the grassland during the study period, and the various aspects of habitat quality and the landscape context of the sites.

I have tried to answer these questions:
Is there a relationship between population size 2005 and the population size recorded in the beginning of the observation period 1993-94?
Are the populations isolated from each other and is there a relationship between the relative area and population size?
Has habitat quality any effects on the population dynamics and extinction rates in *G. campestris*?
Have the soil conditions any significance for the population dynamics in the sites?
How does the present management status affect the population dynamics and extinction in these populations?
Is there a connection between older management regimes and population dynamics and extinction?
How can we conserve the remaining populations?

Methods

The 28 populations situated in the county of Södermanland (Fig.1) in the east of Sweden were visited three times during the summer of 2005. During the first visit in the early summer data were collected about the general appearance of the grassland. During the second and third visit at the end of the summer data were collected on *G. campestris* population size, tree and shrub coverage,

vegetation height, thickness of litter layer, soil condition, soil moisture, topographic relief, management status, management and disturbance.

The populations were surveyed two times and number of flowering *G. campestris* was recorded. The maximum number of flowering individuals of *G. campestris* was used in the analyses. A source of error could be the time of the survey of the populations. For example I got two very different results for Mora Gård (counting two times with three weeks apart) suggesting that the time of the counting could play a major role for the result of the size of populations.

The isolation were assessed by measuring the distance to the closest population N_{2005} >1. The relevant area, possible growth-area of *G. campestris* in a site, was assessed by measuring the area (in ha) on the Economical map.

The tree and shrub coverage were assessed by identifying trees as woody plants over 3m in height and shrubs as woody plants below 3m in height, including all *Juniper communis*. Using inventory methods according to Jordbruksverket (2005) I used three classes of cover to divide the population area: non-some (0-10% coverage), half open-half closed (10-70% coverage) and closed (>70% coverage). I added 5m around the population area to get a more comprising description of the area. If the population area included more than one class of cover the area was divided into given 10% classes adding up to 100% (rounding the 6-15% to 10%, 16-25% to 20% etc). Many populations had several large patches and for all patches tree and shrub coverage were assessed as above. In the analysis the patch with most individuals of flowering *G. campestris* represented the entire population in the analysis.

Soil moisture was determined using inventory methods according to Jordbruksverket (2005). Four classes were used; “dry” constituted of typical species like *Festuca ovina, Luzula campestris, Saxifraga granulata, Helictotriochon pratense, Antennaria dioica, Taraxacum* sect. *Erythrosperma, Pilosella officinarum*; “mesic” constituted of typical species like *Agrostis capillaris, Alchemilla sp., Plantago lanceolata, Trifolium sp.*; “moist” constituted of typical species like *Deschampsia cespitosa, Filipendula ulmaria, Geum rivale, Taraxacum* sect. *Palustria, Galium palustre, Galium uliginosum*; “wet” constituted of typical species like *Ranunculus flammula, Ranunculus sceleratus, Triglochin palustre, Alopecurus geniculatus, Glyceria fluitans, Phragmites australis* and a dominance of *Carex* species. Like in the tree and shrub coverage I added 5m around the population area or the patches. If there were different classes in the area of the population, the area was divided into given 10% classes adding up to 100% (rounding 6-15% to 10%, 16-25% to 20% etc). The

patch with most individuals of flowering *G. campestris* represented the entire population in the analysis.

The topsoil was assessed by an ocular inspection. A 0.25 x 0.25m, and 0.3m deep hole was dug close to each population. In sites lacking a population, holes were dug in the most likely places of a population of *G. campestris*. The soil samples were dived into four classes; “clay” including silt and clay, when rolling between fingers forming a roll; “till with unsorted material” had a coarse character; “wave-washed till” had a smooth character; “bedrock” had less then 0.05m of topsoil. I also assessed the topsoil layer in the sites as homo- or heterogeneous, and the relief of the location of the population, as horizontal or sloping (small or large). I also assessed the aspect, grouped into five categories: east (45º-135º), south (135º-225º), west (225º-315º), north (315º-45º), and horizontal. I supplemented the topsoil assessment with maps from Geological Survey of Sweden (SGU Ae).

The management status of the grasslands in general and at the population site was assessed by looking at the area if it was well mowed or grazed, if there were none or much litter and if there were woody plants in the open areas. A “well managed area” was mowed or grazed and had no litter accumulation and no woody plants, a “weakly managed area” had reduced grazing or mowing with litter accumulation as a result and woody plants in open areas, and “no management” implies no grazing and a large amount of litter and encroachment by woody plants. Like above I added 5m around the population area or the patches and the classes of management in the population area were divided into given 10% classes adding up to 100% (rounding the 6-15% to 10%, 16-25% to 20% etc). Management status at the population site was also assessed by measuring the vegetation height and litter accumulation using a sward stick in a quadrate 5x5m, a total of 30-36 samples per site.

By talking to the landowners or the leaseholder I got information about how many livestock they hade on average during the last 10-year period and if there have been any cessation in the management or when the land ceased to have any management. I also got information about livestock and grazing periods and the management of the grassland. This information about the history and management of the 28 sites was complemented with studies of District maps from 1900-1901 and Economical maps from 1958 and later.

Statistics

All statistical analyses were performed with Statistica 6.0. The relationship between population size (excluding extinct populations), the mean number of *G. campestris* in the years 1993-1994 and in the population size in 2005 was analyzed with a linear regression. Relationships between population size and area and population size and isolation were examined using the median, maximum population size (during 1993-2005) and population size 2005, and analyzed with a linear regression. The difference between extinct, small and large populations concerning isolation and area were analyzed using Kruskal-Wallis ANOVA by ranks and Median test, with three different categories based on median number of *G. campestris*, small: <50 individuals, large: > 51individuals and extinct: if no *G. campestris* was found at the last two records of the population. Relationships between population size and vegetation height and litter height were examined using the median, maximum population size (during 1993-2005) and population size 2005, and analyzed with a linear regression. The difference between extinct, small and large populations concerning litter and vegetation height, were analyzed using Kruskal-Wallis ANOVA by ranks and Median test. Relationships between population size shrub coverage and tree coverage were examined using the median, maximum size of the populations (during 1993-2005) and population size 2005 using Mann-Whitney U-test. Relationships between population size and topsoil properties were analyzed with ANOVA using the median, maximum population size (during 1993-2005) and population size 2005. Relationships between population size and topographic relief and aspect were examined using median, maximum population size (during 1993-2005) and population size 2005, using Kruskal-Wallis ANOVA by ranks and Median test. Relationships between population size and management were examined using the median, maximum size of the populations (during 1993-2005) and population size 2005 using Mann-Whitney U-test.

Site and population description

The description of the sites (Fig. 1) was based on Ängs- och hagmarker i Södermanlands län (Rydberg & Vik 1992) and observations done during the field study and the information from the farmers or landowners.

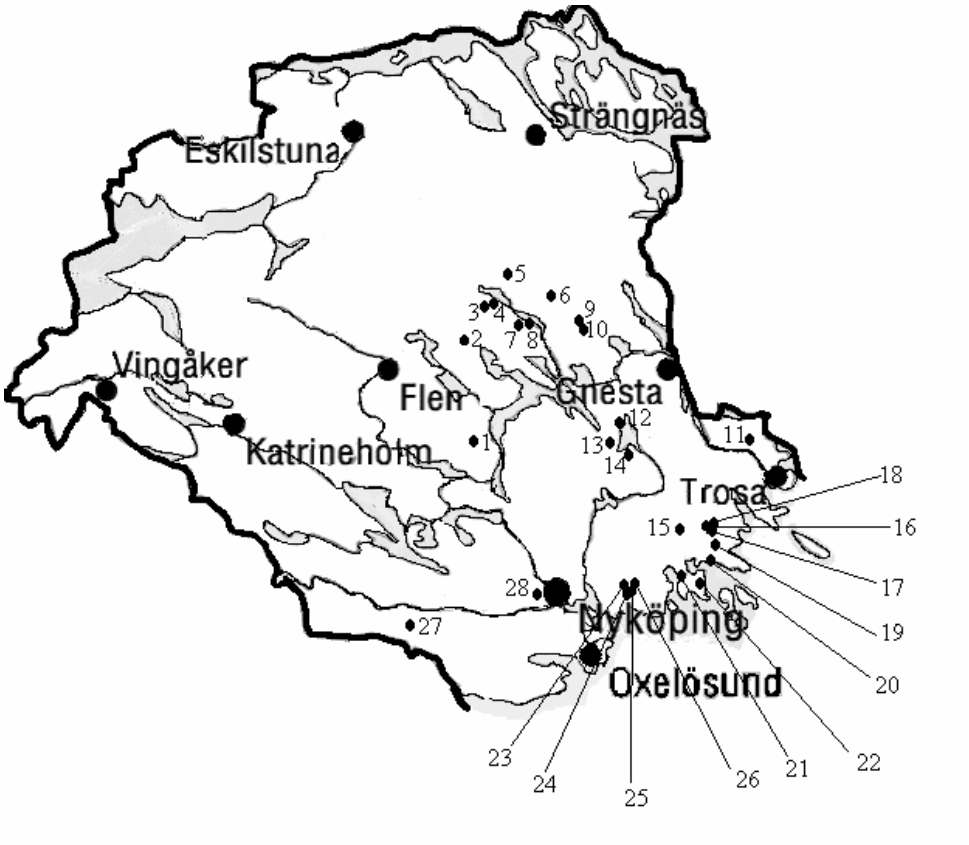


Figure 1. Map showing the location of the 28 sites within the county of Södermanland. 1. Herrgölet, 2. Lyftinge - Stora Råstock, 3. Hässelby - Henäng, 4. Alm-Norräng, 5. Mora Gård, 6. Stora Åsa, 7. Vreta, 8. Herröknanäs, 9. Kärvsätter, 10. Viby (Kesätter), 11. Hunga - Norrgården, 12. Fräkenvassen, 13. Västra Malma - Vreten, 14. Onsberga - Vreten, 15. Grinda - Skyle, 16. Nyckelby - Norrgård, 17. Litselby, 18. Långmaren, 19. Nynäs - Mellanstugan, 20. Nynäs - Sandvik, 21. Hånö säteri, 22. Hånö - Horsvik, 23. Ånga, 24. Björksund - Blindkällan, 25. Björksund - Baggebol, 26. Björksund - Grytmar, 27. Bergtorpsgården, 28. Lindbacke.

1. Herrgölet (N 58º 58' 13.98, E 16º 49' 13.47) is a grassland pasture with a plateau with large birch trees, surrounded with north facing small blocky till slopes with parts of outcrop and a vegetation of *Juniper communis*. In general Herrgölet is well-managed grassland and has been so for some hundreds of years. Before 1995 twenty cattle grazed the grassland pasture and today c. 10 animals graze the grassland pasture. The fewer cattle have influenced the management status of the pasture with parts of high vegetation of grass, litter accumulation and an increasing number of scrubs in the

open areas. The *G. campestris* population was found in the open well-grazed parts of the grassland on the till slopes and around the outcrop.

2. Lyftinge - Stora Råstock (N 59º 5' 27.93, E 16º 47' 20.66) has been a lease farm since at least 1720. The well-managed grassland have for the last ten years been grazed from April in the spring to October in the autumn by around 13 cattle. The *G. campestris* population was growing in the open parts of the enclosure on the more or less sloping sides of till surrounding bedrock with exception for one part of the enclosure that have been an arable field. The mesic vegetation suggests that the moisture in the soil is drained as the topsoil is sandy till, glacial clay and also the topographic relief is slightly sloping.

3. Hässelby - Henäng (N 59º 8' 53.36, E 16º 50' 22.69) has a long continuity of management and has around 8 cattle grazing on and off the whole season April-October. According to Rydberg and Vik (1992) a population of *G. campestris* existed in the grassland 1989. However, no existing population has been found since 1993. The location of the extinct population was in an open nearly horizontal part of the enclosure with small blocks surrounding bedrock with topsoil of clay and sandy till adjacent to a marsh and with a vegetation of both mesic and moist herbs.

4. Alm - Norräng (N 59º 9' 12.59, E 16º 50' 42.15) close to Hässelby - Henäng is in some parts a well-managed grassland with 5-9 cattle grazing April-October. Alm - Norräng has a long continuity of management. The grassland gives a heterogeneous impression with an undulating landscape and open to closed vegetation of birch and junipers with topsoil varying from sandy till to clay. *G. campestris* was found on the sloping sides of a hill with outcrop and on a clay bank connected to the hill.

5. Mora Gård (N 59º 11' 13.62, E 16º 54' 19.96) is an open meadow with birch and junipers, gently sloping towards a small creek and a lake. The floral species richness indicates a long history of management, and today a total of 20 cattle graze the meadows on and off from May-October. In the beginning of the summer and the first visit to Mora Gård it was little grazed and at the last two visits not grazed at all. The large population of *G. campestris* was found in the open and stony parts of the meadow with topsoil of sand and sandy till.

6. Stora Åsa (N 59º 9' 30.87, E 17º 2' 5.50) includes four enclosures with partly restored old pastures, and a new enclosure on a former arable field. The flat pasture with small blocky sandy till includes parts of pine forest and marshland and in all four enclosures *G. campestris* was found in

the more open areas with a stony character but also on the former arable field. Species richness indicates a long continuity of grazing probably without any breaks in management. However, the number of animals grazing was only 6 cattle May-October and 20 sheep grazing after the cattle.

7. Vreta (N 59º 6' 57.86, E 16º 55' 11.48) has, according to the owners, been a farm since the beginning of the 20th century and probably earlier than that, with cattle grazing the adjacent pastures. In the year 2000 the 12 cattle were replaced with 20 sheep that now graze the pasture. Until 2001 one of the two enclosures had a population of *G. campestris*. However no individuals could be found during the field study. The flat surface sand and till still contains a number of semi-natural grassland species but the area, with the presumably extinct population of *G. campestris*, has become overgrown with high vegetation of shrubs and grasses and with a large litter accumulation, as a result of the sparse grazing.

8. Herröknanäs (N 59º 7' 0.16, E 16º 56' 58.40) had according to maps from 1821 agriculture on the land and prehistoric finds in the area indicates a long continuity of management. For a long time beef cattle grazed the pastures and the mown hayfields and the land was well managed until 1985-90 when declining number of grazing cattle resulted in an overgrowth of shrubs in the grassland. It was restored 1993-97 and became a protected area in 2001 and is now managed traditionally, hayfields are mown and later grazed by 20-30 cattle May-September. The large enclosure is characterized by two plateaus of outcrop and till, an open landscape with hayfields, large oak trees and wet pastures by the lake Misteln. *G. campestris* had not been found since the inventory in the late 1980's and was not found during the last visit (1994). However on a hill of glacial clay and till, among junipers and birch a small population of *G. campestris* was found during the field study.

9. Kärvsätter (N 59º 5' 56.12, E 17º 4' 34.87) has probably a long history of management and was grazed by cattle until 1993 but for the last ten years Kärvsätter has had little or no management. The previous (now extinct) population of *G. campestris* grew in an open area of the pasture, with blocky, sandy till and glacial clay, that still contains some rare semi-natural grassland species.
10. Viby (Kesätter) (N 59º 5' 39.69, E 17º 5' 2.53) was grazed by horses until 1997 and is today an abandoned pasture. The northwest facing till slopes have become overgrown with birch and high vegetation of grasses and have a large litter accumulation. The surviving population of *G. campestris* is growing on a footpath on a small hill of outcrop surrounded with sandy till with fairly open vegetation.

11. Hunga - Norrgården (N 58º 55' 20.60, E 17º 30' 54.76) is characterized by a ridge of outcrop with wave-mashed sandy till and an old arable field. The management history is most likely long as the floral species richness is high and the grassland is still very well kept with 10 cattle grazing throughout the season. In a corner of the enclosure, in a well-grazed area with topsoil of sand, a small population of *G. campestris* was found 2001. Today the population is probably extinct.

12. Fräkenvassen (N 58º 59' 30.82, E 17º 10' 58.37) has a long management history and has been a farm since 17th century according to the owner. 1930-1950 the grassland pastures were grazed by milk cows and before that it was a pig farm. Today 18 cattle, 18 sheep and also 4 horses graze the pasture and are moved around to different enclosures during the season. The pasture with ridges of bedrock with slopes of till along with old arable fields and hayfields give an undulating character to the landscape. According to Rydberg and Vik (1992) *G. campestris* could be found among with other rare semi-natural grassland species but has not been found since their inventory in the late 1980's.

13. Västra Malma - Vreten (N 58º 57' 28.45, E 17º 7' 39.53) has according to the landowner been grazed by cattle since the 1920's and before 1997 when management ceased, 7 cattle grazed the grassland. In 1998 the population of *G. campestris* still existed and was found in leveled area partly under a power line next to arable fields. The open area with topsoil of fine sand has become overgrown with bushes and dense forestation, some parts are still open and species-rich but with much litter accumulation.

14. Onsberga - Vreten (N 58º 54' 58.22, E 17º 12' 40.00) is most likely a very old grassland pasture that has been unmanaged since 1997 and is slowly becoming overgrown with trees and bushes. In the open parts of the grassland in the slope of sandy till and glacial clay a population of *G. campestris* still occurs. The larger part of the population was found in the edge of a wood, a dry slant covered with *Pilosella officinarum*, the other part was found on and around a small hill with high grass vegetation.

15. Grinda - Skyle (N 58º 49' 52.08, E 17º 18' 29.18) has been managed continuously since the late 19th centuries but it is named in documents from the 14th century according to the owner. 12-15 milk-producing cattle grazed the grassland until 1960, now 20 meat-producing cattle graze the entire area during May-October. The whole grassland is today open for grazing but before the 1960's the grassland had smaller enclosures and was grazed in turns. The small *G. campestris*

population was found alongside the road that passes through the grassland in an open area around a hill where the terrain is small blocky till and topsoil is of wave-washed sandy till.

16. Nyckelby - Norrgård (N 58º 50' 21.34, E 17º 22' 46.10) was colonized during the late Iron Age (500-1050 AD). The long continuity of management has resulted in species-rich grasslands and an open to half-open character with large birch and pine trees. In the open small blocky terrain around a burial-mound the *G. campestris* population was found. Around 20-30 cattle graze the grassland on and off the now enlarged enclosure.

17. Litselby (N 58º 49' 59.52, E 17º 23' 25.64) (as Nyckelby-Norrgård) was probably colonized during the late Iron Age (500-1050 AD) and farming and agriculture was the main livelihood but was complimented with fishing and hunting. The grassland has a long management history and is still managed with cattle grazing on and off the season. The small population of *G. campestris* was found in the north facing steep slopes with fine sand and varved clay surrounding outcrop. This part of the grassland is well managed and open with a few junipers, in the other parts it's beginning to get overgrown with bushes.

18. Långmaren (N 58º 49' 54.20, E 16º 24' 30.85) has a long continuity of management and was documented on maps 1667. Långmaren is still managed in an elderly fashion, now as a museum farm. The grassland consists of 20.5 ha old arable fields and islands of outcrop and around them blocky, sandy till and varved clay. 20 cattle graze the hay fields/grassland pasture on and off the whole season. The population of *G. campestris* was found around these pine-covered islands of outcrop and till, spread out in the whole grassland pasture.

19. Nynäs - Mellanstugan (N 58º 49' 7.24, E 17º 24' 38.03) is an open grassland pasture that consists of old arable fields and a wooded area. The terrain is of outcrop surrounded with blocky till and topsoil of varved clay, and vegetation dominating of junipers. According to the Economical map the arable fields were still in use 1958. Before 1998, when there was a break in the management for one or two years, cattle and horses grazed the grassland. Today the grassland is grazed by 8 cattle the whole season and also sheep. The one *G. campestris* was found near one of the arable fields in a slightly sloping blocky part of the grassland.

20. Nynäs - Sandvik (N 58º 47' 41.67, E 17º 24' 30.97) consists of a heterogeneous landscape including some old arable fields, an old hayfield and now including a large forest as the enclosure has been enlarged. The population of *G. campestris* was found in mostly open grasslands around

islands of outcrop and topsoil of varved clay. The species richness of the flora in the grassland and hayfield indicates long management continuity with grazing and mowing. Today cattle graze the grassland, at what extent was hard to assess during the field study.

21. Hånö säteri (N 58º 46' 52.94, E 17º 20' 53.94) was a large enclosure of 21.9 ha of forest and open grassland pastures and, before management ceased sometime in the 1980's, grazed by cattle. In 1993 two *G. campestris* were found in an area with outcrop surrounded with wave-washed till. The site was probably open grassland longer than the surroundings but now it is more closed with tall trees and large juniper shrubs.

22. Hånö - Horsvik (N 58º 45' 33.21, E 17º 23' 22.84) is situated by the Baltic Sea, surrounded by species-rich pastures and hay fields that have been in the same family's ownership for 180 years. It has been grazed mainly by sheep and cattle and some parts were mown for fodder. The grazing of sheep ended three years ago and the land is showing signs of overgrowing with shrubs and litter accumulation. The population of *G. campestris* is dispersed in an area with outcrop surrounded with wave-washed blocky till with topsoil of gravel, slightly sloping to the east and half-open to open.

23. Ånga (N 58º 44' 46.32, E 17º 11' 44.21) has a long continuity of management and is today grazed by around 50 cattle that are moved around to different enclosures during the season April-November (December). The enclosure consists of an old arable field or hayfield and a small blocky pasture that has a wave-washed surface of sandy till. In the well managed pasture the scattered population of *G. campestris* was found in mostly half-open areas with mesic vegetation but also on small and dry knolls of *Pilosella officinarum* ssp. *pilosella* overgrown blocks.

24. Björksund - Blindkällan (N 58º 45' 42.11, E 17º 12' 54.87) is an open pasture with a dominating plateau of outcrop that has a number of large solitary pine trees, *Pinus sylvestris*. The much sloping sides of the plateau of blocky wave-washed till had a high vegetation of *Pteridium aquilinum*. In the more grazed parts of the till sides, the population of *G. campestris* was found. In 1994 the landowner changed management from milk cows to meat producing cattle. The pasture includes an arable field that is the first part of the total enclosure to be grazed the first week of May. Later in the season, around 5 cattle graze the old pastureland. It has at least been grazed for 50 years but probably for much longer.

25. Björksund - Baggebol (N 58º 45' 14.17, E 17º 13' 37.28) has a long history of management and has been continuously grazed since the 18th century according to the owner. During the last ten

years there have been approximately 4 cattle and some horses grazing the pasture May-October. The open pasture has a plateau of outcrop with sides of blocky wave-washed sandy till, with bushy vegetation of *Pteridium aquilinum* and *Calluna vulgaris*, and areas with leveled surface with varved clay where most of the *G. campestris* population was found. Fewer were found in the sloping till sides.

26. Björksund - Grytmar (N 58º 45' 38.63, E 17º 15' 42.70) consists of two well-managed grassland pastures that are grazed by 50 cattle that are moved around the pastures throughout the season Mars-November. The pasture where the small population of *G. campestris* was found consists of a small blocky till landscape with wave-washed topsoil of sand and open vegetation is of junipers, hazel (*Corylus avellana*) and birch. The pasture is now larger than the enclosures in 1993 and includes former arable fields.

27. Bergtorpsgården (N 58º 42' 52.85, E 16º 37' 54.33) is a nutrient poor species-rich grassland pasture with long management history of grazing and mowing. According to Rydberg and Vik (1992) the management was meager after 1990 and the pasture lacked management during 1991-1992. In 1996 the population of *G. campestris* could be found in the whole enclosure. However, no individuals were found during the field study 2005. The slightly undulating small blocky pastureland has a topsoil of postglacial coarse silt, sand and gravel and open vegetation of solitary birches and *Salix repens* and is today grazed by around 15 cattle.

28. Lindbacke (N 58º 44' 34.42, E 16º 59' 11.36) is a large hill of bedrock with outcrop surrounded with sloping sides of wave-washed sandy till. *G. campestris* was found in the moor like landscape on the south side, an oligotroph dry pasture with great species richness. Findings from the Iron Age (500-1050 AD) indicates that Lindbacke was used together with surrounding areas for farming and agriculture and the pastures were mown to provide the cattle with hay over winter (communication Camilla Erlund, 2005). This long management history has more or less been continuous until 1960's. Under a period the area became overgrown with shrubs and high vegetation but in 1981 the area became a nature reserve and was restored in 1988 and 1993. Today Lindbacke is grazed by cattle.

Results

Population dynamics

During the 13 years (1993-2005) the populations have been recorded, the population size within the 28 populations have fluctuated differently and in some populations substantially. Some populations have become extinct (Fig. 2), others are close to becoming extinct (Fig. 3-6). To clarify the fluctuations in populations size in the years 1993-2005, all populations have been divided into five different categories according to median number of *G. campestris*, very small: <10 individuals (Fig. 3), small: 10-50 individuals (Fig. 4), intermediate: 51-100 individuals (Fig. 5) and large: >100 individuals (Fig. 6). If no *G. campestris* was found at the last two records the population was presumed to be extinct (Fig. 2). There is no information about the years 2000, 2003 and 2004 as no field studies were performed these years and for some sites there are gaps in the dataset 1997-99 and 2002.

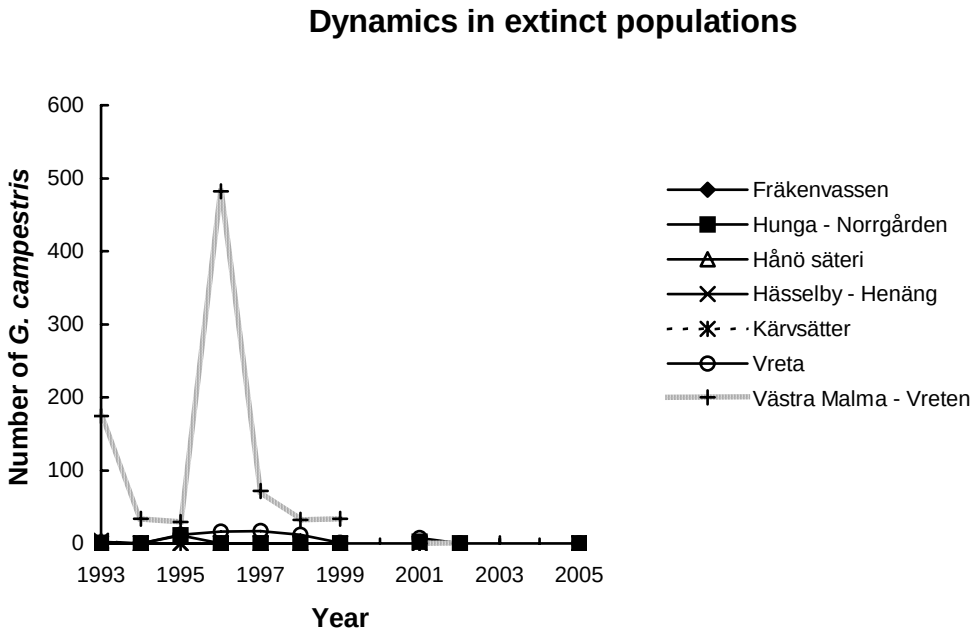


Figure 2. Population dynamics in now extinct populations of *G. campestris* (no observed individuals the last two records) based on the number of individuals in populations from 1993-2005.

The 7 populations in Fig. 2 are presumed to be extinct. According to field data Hässelby - Henäng and Fräkenvassen lacked populations already at the first observations 1993. Kärvsätter had 4 individuals 1993, and Hånö säteri had 2 individuals 1993, and at both sites no more individuals were recorded after that occasion. Hunga - Norrgården had in 2001 a small population of 2 individuals and Vreta had a population of 7 individuals. Västra Malma - Vreten had a relatively large population until 1999 but no population has been recorded since that year.

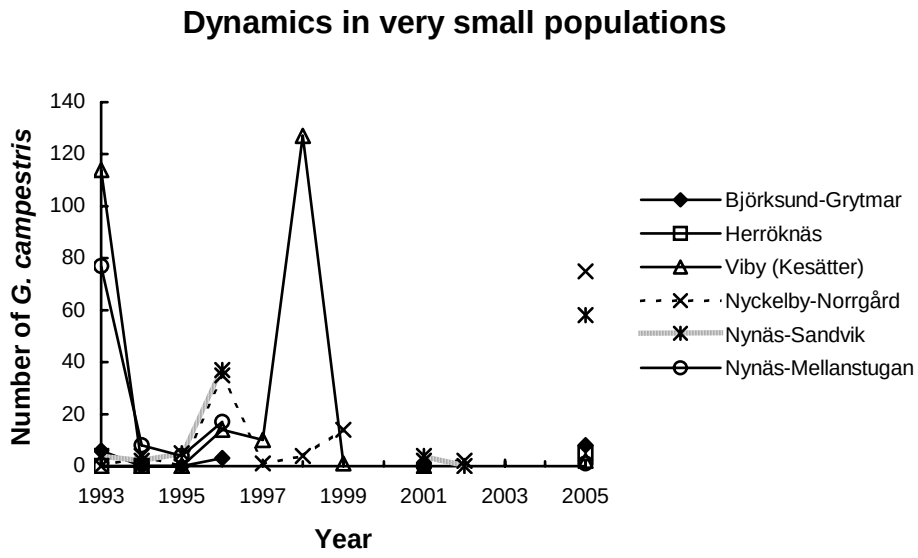


Figure 3. Population dynamics in very small populations of *G. campestris* (median number of individuals <10) based on the field records 1993-2005.

Herröknanäs (Fig. 3) had no population in 1993 and 1994. However, this site has not been visited after 1994, but in the present study a small population was found. Björksund - Grytmar, Viby (Kesätter), Nyckelby - Norrgård, Nynäs - Sandvik, and Nynäs - Mellanstugan all have populations (Fig. 3).

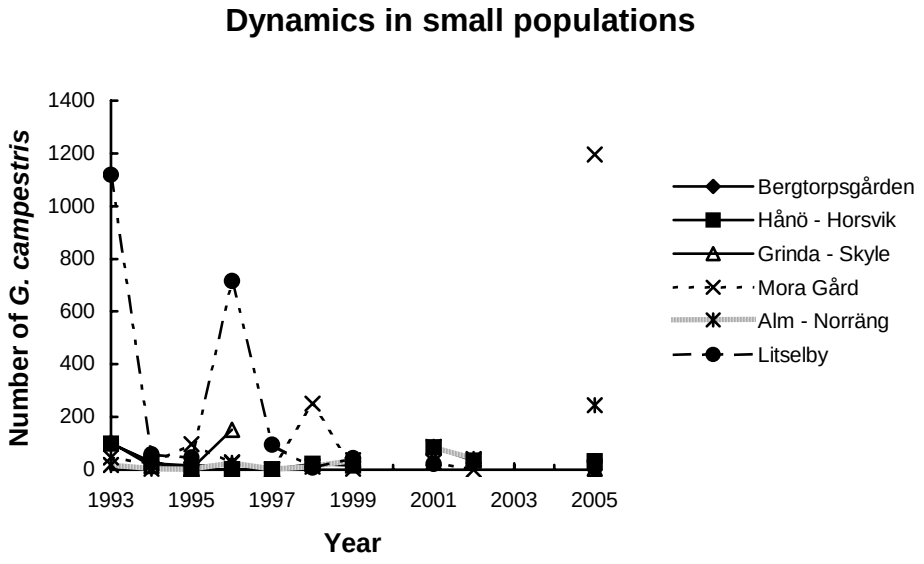


Figure 4. Population dynamics in small populations of *G. campestris* (median number of individuals: 10-50) based on field records 1993-2005.

The populations at Mora Gård and Litselby have fluctuated considerably (Fig. 4). Litselby have gone from 1119 individuals in 1993 and 717 in 1996 to 9 in 1998 and 33 in 2005, and the

population at Mora Gård was zero 1997 and 2002 but had 1195 individuals in 2005. The other populations have had a less fluctuating population size.

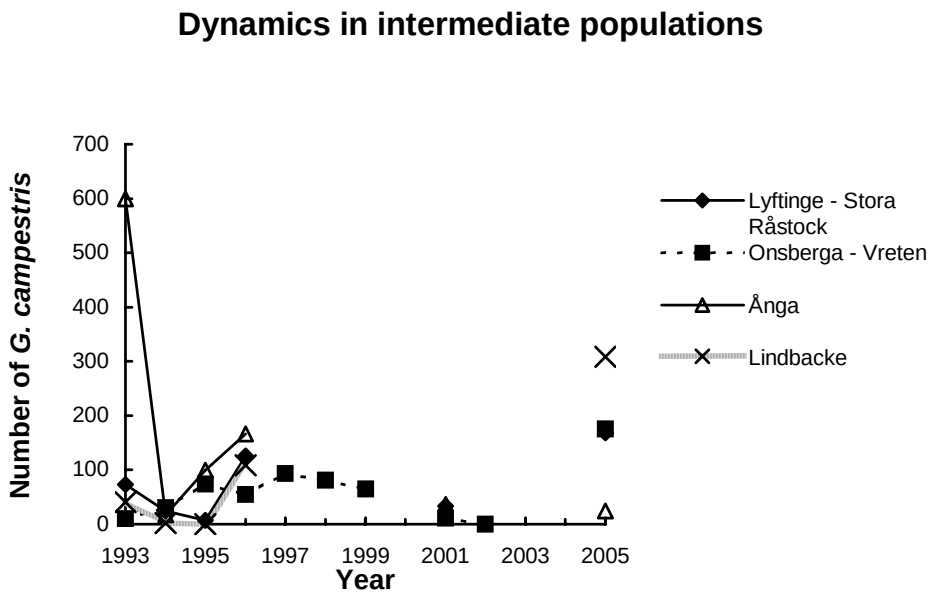
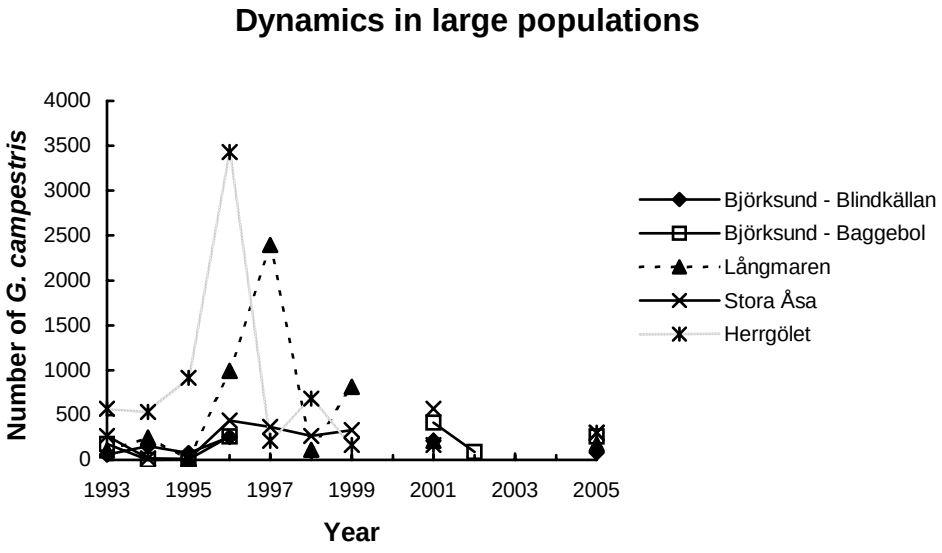


Figure 5. Population dynamics in intermediate populations of *G. campestris* (median number of individuals 51-100) based on field records 1993-2005.

The populations in Fig. 5 have seemingly fluctuated less than the small populations. Ånga had a large population, 600 individuals, 1993, and Lindbacke, in contrast to Ånga, have increased its population's size from 2 individuals 1994 and zero in 1995 to 308 individuals



2005.

Figure 6. Population dynamics in large populations of G. campestris (median number of individuals >100) based on field records 1993-2005.

Fig. 6 shows fluctuations in the large populations. Långmaren had in 1995 only 12 individuals and the next year 995 individuals and 2395 in 1997. Björksund - Baggebol, Stora Åsa and Herrgölet also display fluctuations in population size.

This overview shows that, of the 28 populations, 7 (25%) have become extinct since the initial inventory in the late 1980's, 12 populations (43%) have a median size below 50 individuals, although some of these populations in some years have had more than 1000 individuals, and 9 populations (32%) have a median size above 50 flowering individuals.

Predictions of population size

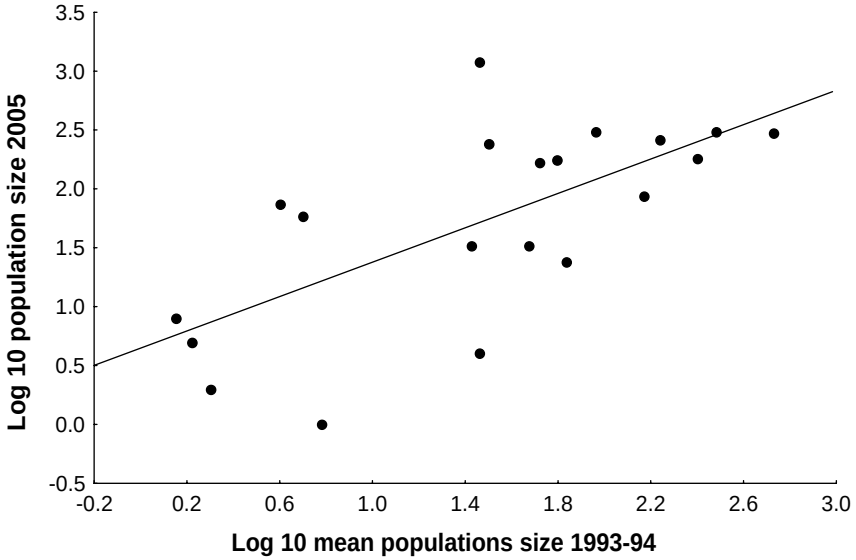


Figure 7. The relationship between population size of *G. campestris* in 2005, and the average population size at the same sites 1993-1994, $r^2 = 0.457$, p = 0.001 (Log10(Population size 2005) = 0.64808 + 0.72967 Log10 (Mean population size 1993-94)).

There was a strong relationship between the population sizes 2005 and the size of the population at the corresponding sites 1993-94 ($r^2 = 0.457$, p = 0.001) (Fig. 7). Thus, although the populations fluctuate widely (Fig. 3-6), there is a consistency over time in the population sizes.

Effects of isolation and habitat area on population size

No significant relationship was found between isolation, the distance to the closest population N_{2005} >1 and the median size of populations 1993-2005 (p=0.54), maximum populations size 1993-2005 (p=0.66), or populations size 2005 (p=0.56).

The habitat area for the populations (possible growth-area of *G. campestris*) was not related to population size: median population size 1993-2005 (p=0.33), maximum population size 1993-2005 (p=0.18), or population size 2005 (p=0.68).

There was no significant difference between the extinct, small and large population and isolation (ANOVA by ranks H=0.54, p=0.76, Median test Chi-Square=0.25, N=28, p=0.88) or area (ANOVA by ranks H=3.96, p=0.14, Median test Chi-Square = 1.26, N=28, p=0.53).

Effects of habitat quality on population size

There was no relationship between mean vegetation height and median population size 1993-2005 (p=0.84), maximum population size 1993-2005 (p=0.90), or population size 2005 (p=0.77). No relationship was found between mean litter height and median population size 1993-2005 (p=0.63), maximum population size 1993-2005 (p=0.33), or population size 2005 (p=0.68).

No significant difference was found between the extinct, small and large population and mean litter height (ANOVA by ranks H=0.92, p=0.63, Median test Chi-Square = 1.73, N=28, p=0.42) or mean vegetation height (ANOVA by ranks H=1.47, p=0.48, Median test Chi-Square=0.59, N=28, p=0.75), analyzed using Kruskal-Wallis ANOVA by ranks and Median test.

The three classes of tree and shrub coverage used in the field were rearranged into two groups, one category "non-some" and one category combining "half open-half closed" and "closed".

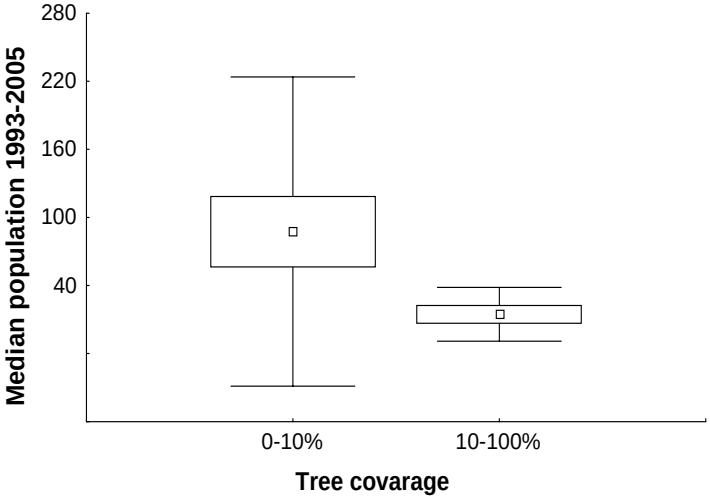


Figure 8. The difference between 0-10% coverage ("non-some") and 10-100% ("half open-half closed" and "closed") tree coverage concerning population median size 1993-2005. Small boxes show mean values, larger boxes range and standard error and crossbars the extent of standard.

There was a significant difference between the groups of tree coverage and both median population size 1993-2005 (U=39, N=28, p=0.022) and populations size 2005 (U=23.5, N=28, p=0.001) (Fig. 8). Large populations of the *G. campestris* were more common in open areas and small and now extinct populations were more common in areas with more coverage of trees. However, there was no significant difference in population size between the two groups of shrub coverage, median population size 1993-2005 (U=71.5, N=28, p=0.24), and population size 2005 (U=65, N=28, p=0.14).

Topsoil from the 28 populations were classified into four classes clay, till, wave-washed till and bedrock (not represented by any population thereby excluded). There was no significant difference in population size between the three topsoil classes, median population size 1993-2005 (p=0.72) or population size 2005 (p=0.96). However more then 45% of the habitats topsoil layer were heterogeneous and consisted of more then one topsoil class.

There was no significant difference between the three classes of topographic relief and median population size 1993-2005 (ANOVA by ranks; H=3.21, p=0.20, Median test; Chi-Square=3.1, N=28, p=0.21), maximum population size 1993-2005 (ANOVA by ranks; H=3.58, p=0.17, Median test; Chi-Square=2.19, N=28, p=0.33), and population size 2005 (ANOVA by ranks; H=5.56 p=0.06, Median test; Chi-Square=5.62, N=28, p=0.06), analyzed using Kruskal-Wallis ANOVA by ranks and Median test. No significant difference between median population size population 1993-2005 (ANOVA by ranks; H=1.95 p=0.75, Median test; Chi-Square=6.17, N=28, p=0.19), maximum population size 1993-2005 (ANOVA by ranks; H=1.42, p=0.84, Median test; Chi-Square=3.43, N=28, p=0.49), and population size 2005 (ANOVA by ranks; H=5.81, p=0.21, Median test; Chi-Square=6.71, N=28, p=0.15) and the five classes of aspect were found.

Effects of management history on population size

Populations at sites with continuous management were compared with populations at sites with interrupted or ceased management, and populations at sites with interrupted management were compared with populations at sites with ceased management (Fig. 9).

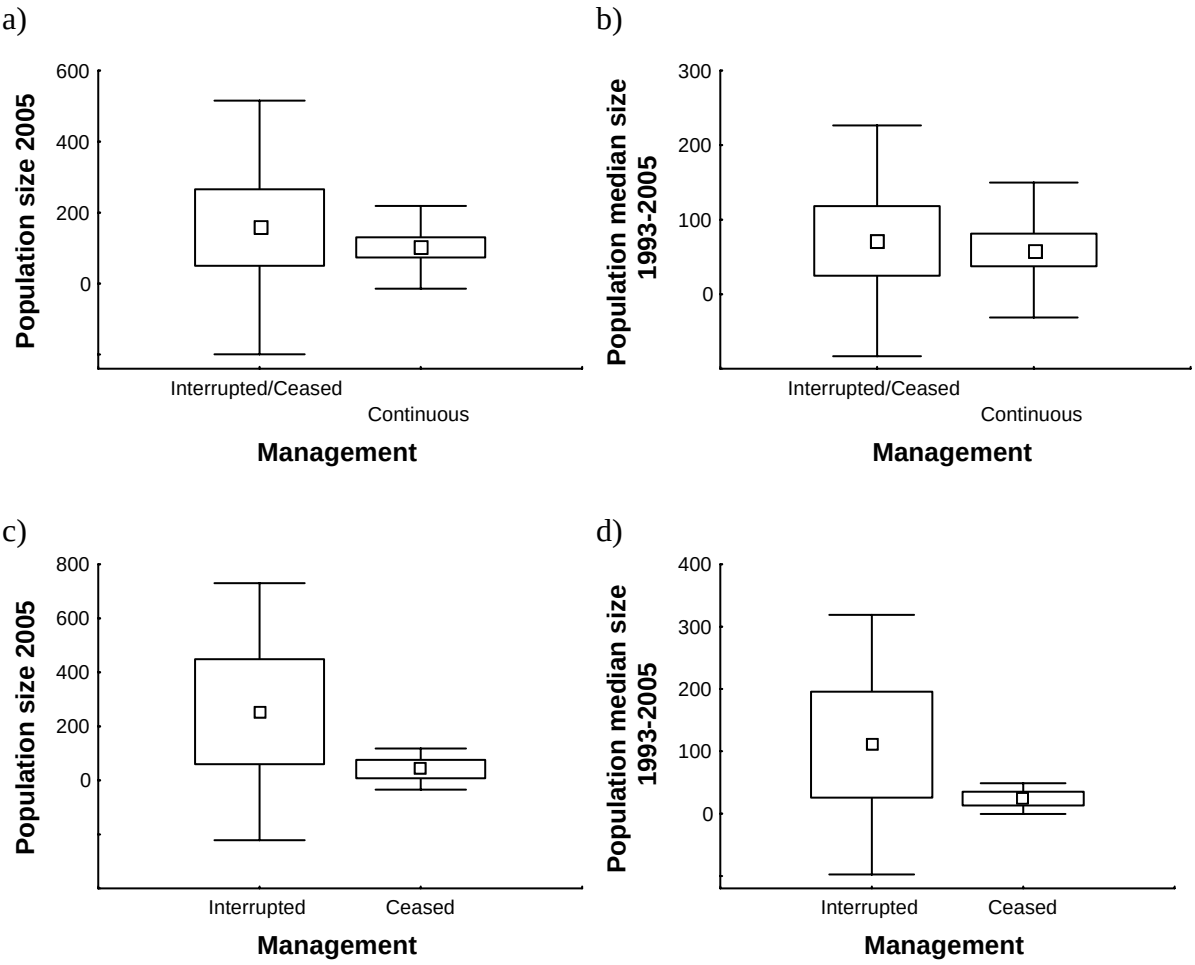


Figure 9 Comparison of the management history at sites with a) population size 2005 with interrupted and ceased vs. continuous management, b) population median size 1993-2005 with interrupted and ceased vs. continuous management c) population size 2005 with interrupted vs. ceased management, d) population median size 1993-2005 with interrupted vs. ceased management. Small boxes show mean values, larger boxes range and standard error and crossbars the extent of standard deviation.

There were no differences in population size at sites with continuous management vs. sites with interrupted or ceased management (median population size 1993-2005; U=87, N= 28, p=0.78; and population size 2005; U=81, N=28, p=0.58). Similarly, there were no difference in population size between sites with interrupted vs. ceased management (population size 1993-2005; U=11.5, N=11, p=0.54; population size 2005; U=11, N=11, p=0.54). Thus, rather surprisingly, the management conditions during the observation period seems to have little general effect on the population size.

However, one should note that the large populations are all located at sites with continuous management. In contrast, small (and now extinct) populations occur both at sites with continuous management and sites with interrupted or ceased management. With one exception (Onsberga - Vreten), ceased management is associated with population extinction. Continuous management is no guarantee for maintenance of a *G. campestris* population (e.g. Fräkenvassen).

Discussion

Population dynamics

The size of some of the 28 populations has fluctuated greatly whereas other populations have remained more stable. Some populations have gone from a thousands individuals to a couple of hundreds, or even less, in one year, and other populations have had some twenty or thirty individuals all the time since 1993. However, overall, the population mean size in 1993-94 is fairly well related to the population size in 2005. An implication of this is that over a large set of populations, one may make relatively good predictions of future population sizes, within a time span of a decade.

Several populations have gone extinct since the late 1980's. Kärvsätter and Hånö säteri are with certainty extinct, the management ceased 1994 and during the 1980's respectively. Also in continuously well-managed sites like Fräkenvassen and Hässelby - Henäng populations have gone extinct. The populations in Vreta and Hunga -Norrgården are interpreted as extinct but may perhaps be alive as these sites are still grazed and had small populations as late as in 2001. Less likely is the persistence of the population at Västra Malma - Vreten. The site has not been managed since 1997, and no individuals have been recorded later than 1999. Despite the lack of relationship between population size and management, abandonment of management, with associated litter accumulation and encroachment most certainly leads to population extinction.

Among the small populations Herröknanäs, Björksund - Grytmar, Viby (Kesätter), Nyckelby - Norrgård, Nynäs - Sandvik, Nynäs - Mellanstugan, Bergtorpsgården, Hånö - Horsvik, Grinda - Skyle, Mora Gård, Alm - Norräng and Litselby, only two, Viby (Kesätter) and Hånö - Horsvik lack management. Viby (Kesätter) is overgrown and the population has declined since the management ceased. Hånö - Horsvik still have a relatively viable population even though the site during the last three years lacks management and have become overgrown with shrubs and high vegetation. These two populations probably will become extinct in the near future unless management is resumed. The other small populations have all well managed sites. However, the size of their populations influences long-term survival as they become more susceptible to e.g. environmental changes. The

populations at Mora Gård and Litselby differ from the other small populations in the sense that they have very pronounced peaks and dips in population size. Possible explanations could be stochastic events like drought in combination with grazing at the wrong time, factors that are likely to rapidly reduce population size.

The larger populations Lyftinge - Stora Råstock, Ånga, Lindbacke, Björksund - Blindkällan, Björksund - Baggebol, Långmaren, Stora Åsa, Herrgölet, Onsberga - Vreten also exhibit fluctuations in population size and except for Onsberga - Vreten all are well managed. Onsberga - Vreten still have a seemingly viable population despite lack of management since 1998. The population is situated on a slope and the larger part of the population grows in a dry area with low vegetation of *Pilosella officinarum*, which could explain the population's vitality although considerable parts of the population grow in high vegetation. Herrgölet, Långmaren and Ånga have pronounced peaks in population size but why Långmaren and Ånga have these peaks is difficult to explain. At Herrgölet the large peak in population size 1996 may be explained by the lack of grazing cattle during years 1995 and 1996. The still low vegetation combined with no herbivores could have given *G. campestris* advantages to grow a large population. The fluctuations in population size in the other large populations are probably due to stochastic demographic and environmental events.

Effects of isolation and habitat area on population size

As no significant relationship was found between the distance to the closest population and population size we can assume that most of the populations are isolated from each other. Inter-population gene flow is probably absent in most of these populations as a result of the fragmentation. Longer distances between populations results in lack of inter-population pollination and seed dispersal. Because the transport of hay from the grassland pastures have been a way to disperse seeds, the change in management regimes from mowing to grazing have stopped one way of gene flow. Also the moving of animals has ceased in semi natural grasslands. Low productive traditionally managed marginal pastures have been abandoned (Lennartsson & Svensson 1996). Today the remaining grassland pastures are grazed the whole season. However, there are a few populations that are situated less than a kilometer apart, Litselby, Långmaren and Nyckelby-Norrgård. These populations could have a possible gene flow as bumblebees that pollinate *G. campestris*, according to Lennartsson and Svensson (1996), can fly up to a 1km. Even if pollination is not a prerequisite to ensure seed set in *G. campestris*, as they are highly autogamous, cross-pollination reduce inbreeding effects and can enhance seed set (Lennartsson 2002). If these populations have cross-pollination, other obstacles like the effect of local fragmentation on plant

pollinator-interactions influence the population viability. Lennartsson (2002) found that seed set decreased in herkogamous plants that were locally fragmented as bumblebees visited them less. In contrast, large grassland sites had a higher abundance of bumblebees and herkogamous plants had a higher seed set. The lack of relationship between population size and relevant habitat area could be explained by local fragmentation as the populations in many habitats experience patchiness (personal observation).

Effects of habitat quality on population size

There was no effect of vegetation or litter height on size of the populations. However the measurements were done in the autumn. Litter height is known to influence *G. campestris* germination and seedling establishment (Lennartsson & Svensson 1996; Lennartsson & Oostermeijer 2001) and to get more accurate results from the measurement of the litter height it should be done in the spring when *G. campestris* germinate and establish seedlings. Comparison of litter and vegetation height between extinct, small and large populations showed no difference. Extinct populations do not have higher litter or vegetation then the other populations. As mentioned earlier extinct populations like Fräkenvassen, Hunga - Norrgården and Hässelby - Henäng are well-managed pastures and only Hånö säteri lacks management.

There was a significant difference between population size at sites with different tree coverage but there was no significant difference in population size among sites with different shrub coverage. All the sites of the populations that are presumed extinct have "half open -half closed" coverage of trees except Kärvsätter that have "non-some" coverage. Nearly all of the other populations have "non-some" coverage of trees except for Herröknanäs, Hånö - Horsvik and Ånga. The coverage of shrubs varies among all the populations and among extinct populations four out of seven sites have "half open -half closed" coverage of shrubs and three have "non-some" coverage. It is not obvious why only tree coverage seems to affect the population size. Also shrubs would affect population size and survival, as habitats become locally fragmented disrupting plant-pollinator interactions with inbreeding depression and a reduced seed set as a result (Lennartsson 2002). Also the light availability influences survival of populations. Lennartsson and Svensson (1996) reasoned that for survival of *G. campestris* the availability of light is most important during the most sensitive life stages germination and seedling establishment. The results may thus indicate that the habitats with small populations could be locally fragmented by trees and suffer from light reduction.

G. campestris populations showed no site specificity and the population size was not related to topsoil, topographic relief or aspect. However, for the topographic relief there was a marginally

insignificant relationship with population size 2005, the population size was larger in large sloping sites. The sites and presumed habitats of the *G. campestris* populations display a surprisingly varied topographic relief and aspect and the topsoil layer in 13 of the habitats is heterogeneous with more then one topsoil class and even the soil moisture shows an assorted picture with dry and /or mesic growth sites.

Management

Surprisingly, no difference was found in population size of continuously managed sites vs. sites with interrupted or ceased management. As mentioned earlier, it is possible that this lack of relationship reflects that management is no guarantee for survival of *G. campestris*. Managed sites may thus harbour small (or now extinct) populations as well as large populations. If management ceases, however, the long-term survival of a *G. campestris* population is very unlikely. The fact that populations with management breaks and some unmanaged populations still are alive suggests that other factors influence the survival and size of the populations. Onsberga - Vreten is one of the populations that have been unmanaged for many years and still have a viable population that probably survive because its located in a open dry area. Viby (Kesätter) is another small population that survives as it grows in a footpath on a dry hill. These populations will eventually go extinct as they with time become more overgrown with bushes and trees. Opposed to Onsberga -Vreten and Viby (Kesätter) there is well managed pasture without management breaks like Björksund - Grytmar that has a small population of a few individuals, and Fräkenvassen with no population left despite a management regime with hard grazing pressure. Nearly half of all the populations with management have grazing all season and the other half have sporadic grazing and only Herröknanäs and Björksund - Grytmar have mowing and grazing close to the habitat of *G. campestris*. None of the populations have traditional management methods with mowing in July and grazing in the autumn, which is known to be favorable for *G. campestris* (Lennartsson & Oostermeijer 2001). Only Mora Gård and Nynäs - Sandvik had to some extent a resemblance of the traditional management during this study, with grazing in July, instead of mowing, and no grazing during the summer. Thus, it is likely that a too heavy grazing pressure, despite being conventionally considered as “well-managed”, is not favorable for *G. campestris*.

To give general recommendations about management in the studied habitats is difficult. A preferred first step would be to resume grazing in Onsberga - Vreten, Hånö - Horsvik and Viby (Kesätter) to ensure population survival. Already extinct populations like Hånö säteri and Västra Malma - Vreten have little left of former species richness and may be too deteriorated to be restored. The traditional

management regime is not necessarily the best way to ensure population survival. Nynäs - Sandvik, Onsberga - Vreten and Litselby have possibly the intermediate phenological ecotypes of *G. campestris*, flowering from June-September, and how traditional management with mowing in July would affect the population survival is difficult to predict. The traditional management regime could be hard to apply as the farmers' economy decides how the grazing is executed and the farmer sometimes has no choice other then to let the cattle graze the same pasture all the season. Also the fact that the *G. campestris* habitats are low-productive land makes it even harder for the cattle farmer to survive on these lands. However some farmers have extended the grassland pastures with old arable fields and could probably change the management regime and mimic the traditional management regime in the intent to increase population size. For example by letting cattle graze late in the season September-October could provide seeds with soil gaps caused by cattle trampling which could enhance germination potential. Also litter accumulation and vegetation height could be reduced to the next season, which could be favorable for seed germination.

How to solve the effects of isolation is probably the most difficult problem. New establishment by sowing seeds have shown to been difficult (Eriksson & Ehrlén 2001) and sowing seeds into existing populations can have a negative effect on the native population resulting in outbreeding depression (Fisher & Matthies 1997) and loss in fitness caused by loss of local adaptations. I believe it is a great need to further investigate the management regimes to assess how survival of the studied populations is affected.

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