Effects of sheep grazing on bumblebee flower visitation rate in an alpine ecosystem

– no bees were killed during this experiment –

A B S T R A C T

…...

A permanent landscape scale grazing experiment was established at Hol, Buskerud, in a lower alpine ecosystem with a recent history of rather low grazing pressure. Since 2002, nine sub-enclosures has been permanently subjected to either of three treatments of sheep grazing pressure: grazing-ceased, grazing-maintained and grazing-increased. By applying a transect based study-design with 15 replicates for each treatment, I investigated how bumblebee abundance responded to the grazing gradient. The effect of grazing treatment on bumblebee flower visitation rate was analysed in a glmmADMB model setting together with a number of other independent variables. The grazing-maintained treatment had the highest flower visit count with 260, while the grazing-ceased treatment had 223, and the grazing-increased treatment had 166. However, the conclusive "best model" disregarded grazing treatment as an explanatory factor, partly due to naturally occurring variation in in real time bumblebee distribution. I conclude by putting my findings into a grazing ecological context.

…...

Table of contents:

…...

1. Introduction

As a master student to be, and a passionate bumblebee enthusiast, I was delighted when I was given the opportunity to do research on bumblebee assemblages as part of a large scale grazing experiment at the mountains of Hol, Buskerud. In my introduction, I will first present grazing practices in the context of society, and then introduce the grazing experiment at Hol thoroughly, as much of the subsequent text rests upon this information. Thereafter, I will spend time exploring grazing and plant community responses, mainly in alpine settings, thus putting my work thoroughly into a grazing ecological context. I round this section off with a look at alpine bumblebees before I present my aims.

1.1 <u>Historical background and present day context of grazing practices</u>
Livestock grazing during the summer months has a long history in Norway. Traditionally this has taken place in mountain grazing areas marginal for other uses, thus constituting an important component of local farm economies and a basis for the much of the Norwegian settlement pattern.

When Norway was colonized after the last ice age, this was done by wild flora and fauna, humans and domesticated animals in concert, in such a fashion that human activity has facilitated suitable habitat for many species. Thus, human activity, rather than being an exclusive threat to biodiversity, also forms a basis for the existence of a whole suite of ecosystem types, collectively known as the *cultural landscape*. It is fair to denounce mountain grazing areas as semi-cultural, while the actual proportion of wilderness in Norway (as by definition) is ~5% (DN-rapport, 6-1995). The realization of this is followed by the coming trend that nature conservation is not just something that can be limited to protected areas, but rather should be tightly connected with how we interact with our surroundings, including resource management.

The managed use of mountain grazing areas in Norway has been documented as far back as the Bronze Age (Kvamme, 1988; Moe *et al*., 1988). Also, mountain areas in Norway and much of Europe have an evolutionary history of natural grazing (Körner, 2003), thus the ecosystems in question have been shaped by the long term interplay between natural elements and domesticated/semi-domesticated livestock. But the presence of large herbivores, in numbers and species composition (grazing habits), has been highly varying in time and space, and the actual grazing history of a locality is likely to be important for the effects of future grazing (Augustine & McNaughton, 1998).

2

As with agricultural practices in general, the use of mountain areas for livestock grazing is affected by trends in agriculture and incentives given by political guidelines. The introduction of chemical fertilizer and substantial use of subsidized feed concentrate are relevant examples as well as large carnivore policies. Norwegian farms have, since the 1970's, been shut down at an alarming rate, and while the affected farmed areas have been mostly upheld by fusion into bigger units, this is now less and less the case. Many marginal areas have been abandoned already, and succession is evident throughout the country. The practice of mountain field grazing though, show less decline; but inaccessible areas are likely to be dismissed if more productive lowland areas become available. Some localities though have been subject to intensified grazing regimes in recent times. Also, the overall composition of livestock used in mountain grazing has changed radically since the middle of the 20. century; away from a diverse crowd of sheep, goats, cattle and horses to now almost exclusively sheep.

Large herbivores affect ecosystems by grazing, trampling and defecation , and plant communities show differentiated responses to different grazing intensities (Augustine & McNaughton, 1998; Mysterud & Austrheim, 2005). Therefore, it is of prime importance to investigate the effects different grazing practices, and changes in these, might have on the biological composition of mountain grazing areas, as it is of general interest that these areas can sustain support for future grazing and/or other primary production goals (including berry harvesting) and maintain biodiversity at local and regional scales, as well as provide aesthetic qualities and recreational use.

But why focus on farming and livestock grazing in a pollinator context? A substantial amount (~44%) of the *norwegian red list of species* is made up by species dependent on the open *cultural landscape* (Kålås *et al.*, 2010), which is highly dependent on these managed practices. A fair proportion of these species can be assumed to be important pollinators, as flowering plant abundance has been plunging. Of a total of 207 wild bee species in Norway, about one in three is on the red list, while 12 are considered extinct (Artsdatabanken, 2015b). While mountaneous heathlands are still mostly intact, and by that its pollinator communities, changes in livestock management might influence this for better or worse. In addition, plant community composition is under the influence of (and increasingly affected by), other external factors like accelerating climate change and long transport atmospheric pollution. In conclusion, relevant management recommendations, as guided by several objective and subjective

3

aspects and goals, must be informed by consideration of several external factors co-influencing on the whole of this nature system. One important such aspect is the health of the pollinator community.

1.2 The grazing experiment at Hol

In 2001, a permanent landscape scale grazing experiment was established at Hol municipality, Buskerud county, south Norway (between 60°40' – 60°45' N and 7°55' – 8°00' E). The 2.7 km^2 field area (Figure 1a) is situated in a south facing hillside, ranging from ~1100 to ~1300m a.s.l; the core of the area can be classified as lower alpine climatic zone, while bordering the tree-line ecotone at its lower parts. It consists of a fine scale mosaic of distinct vegetation types of varying grazing value, including *moss-* and *grass snow-beds, lichen heath* and *dwarf shrub heath, low herb- and tall forb meadow*, *bog* and *fen* as the most important in this setting. The site is, by its geological and climatic conditions and relatively moderate productivity, representative for much of the mountain grazing areas of southern Norway. Prior to the experiment, the tree line had been steadily advancing into the lower parts of the field area.

The field was fenced and subdivided into nine (A - I) adjoining areas (from now on called sub-enclosures), each approximately 300 m wide and 1 km deep, such that each sub-enclosure spans most of the elevation gradient. Before grazing started, vegetation type mapping was done at the resolution scale of 2 ha (Figure1b), from which grazing capacity was estimated, and importantly, all the relevant vegetation types are present in similar amounts in the nine sub-enclosures (Rekdal, 2001). Each of the nine sub-enclosures has since 2002 been permanently subjected to either of three treatments of sheep grazing pressure:

grazing-ceased , grazing-maintained (25 sheep/km^2) , grazing-increased (80 sheep/km^2).

Although actual sheep densities were adjusted to vegetation type estimates, i.e. bare rock was subtracted from the area, and vegetation types were differentially weighted for grazing quality. The grazing-maintained treatment represent the historic grazing intensity at the site, which is thought to be ~10-20 sheep/km^2 (Speed *et al.*, 2013) since the shieling practice was shut down around 1970. The grazing-increased treatment represented the highest "sustainable" use of available production capacity.
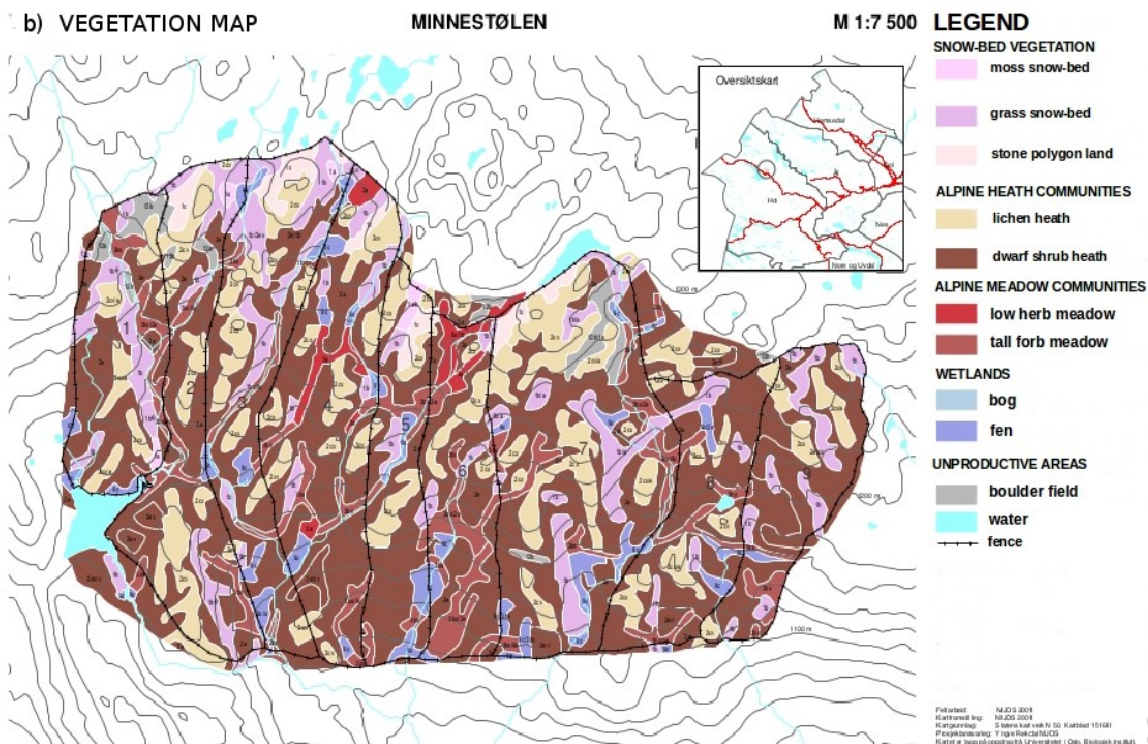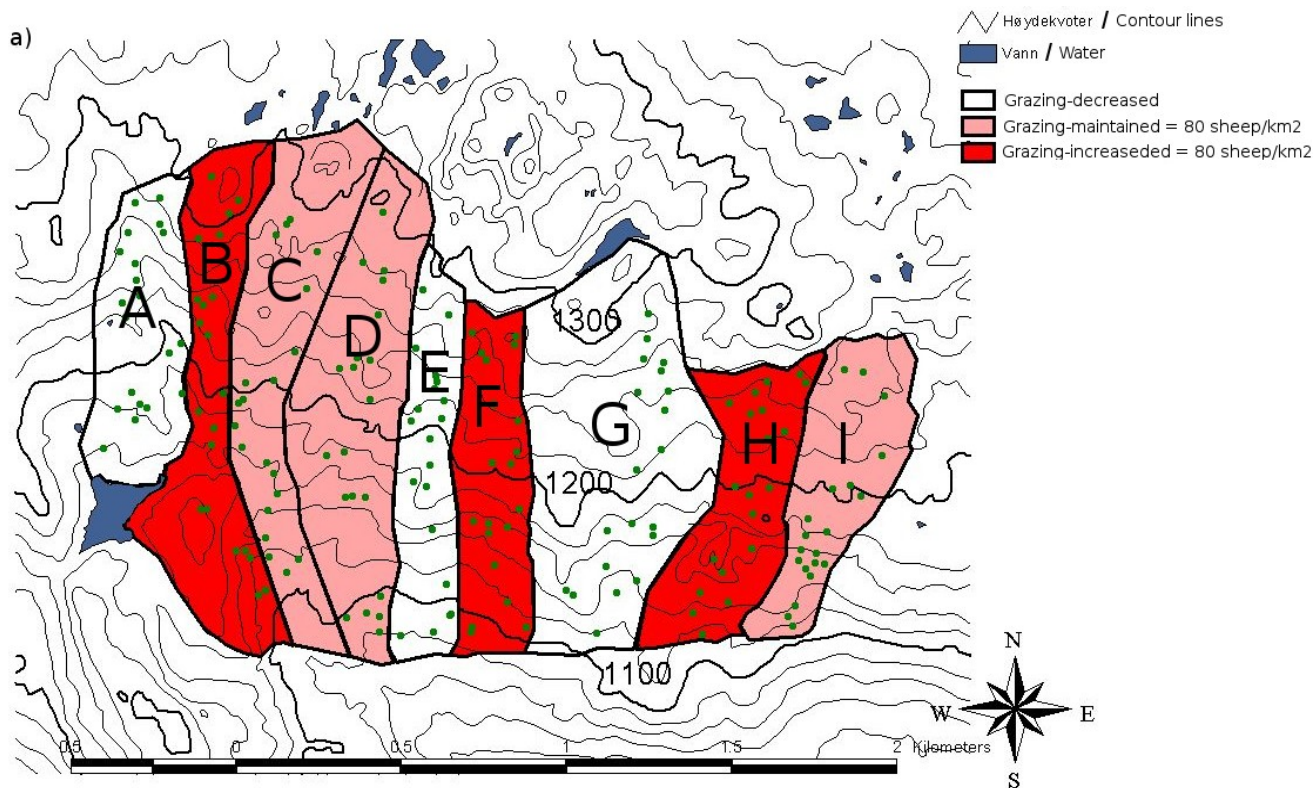
4

Figure 1. a) The experimental field at Hol, with nine sub-enclosures A-I. Colour codes indicate grazing treatment; note that within each block (ABC, DEF, GHI), the three sub-enclosures received different treatments. b) Vegetation map of the field area based on a coarse scale registration excluding areas of < 2 ha. A more fine scale structure exists.

5

Since the vegetation at the field show a small change from east to west, assigning the treatments was done in a block-wise (stratified) random manner, i.e. the field was split into three blocks (sub-enclosures A, B and C constituting the ABC block, likewise for the DEF- and GHI block). Within each block the three sub-enclosures received different treatments.

The aim of the initial project was to evaluate differentiated changes in the alpine ecosystem in response to the three different grazing intensities, as well as mapping accompanying sheep behavior and physiological responses. Background and short term results from the project is well documented in the extensive report: *Økologiske effekter av sauebeiting i høyfjellet. Korttidseffekter.* (Mysterud & Austrheim, 2005). Showing that sheep grazing affects plant demographic prossesses, the authors evaluated the effect on other wildlife by looking for responses across the food chain.

Investigated herbivore/plant feeder taxa were two species of small rodents and selected invertebrates from three insect orders: *Hemiptera, Diptera* and *Coleoptera*. Possible cascading effects onto carnivores and decomposers were investigated using representatives from the same insect orders, as well as *Arachnida.* Some direct effects of resource competition were evident on the herbivore assemblages, while the spillover effects to other functional groups were weaker. Importantly, it was made clear that the effects of grazing are highly context dependent, and that species respond in a complex way to a set of environmental gradients, grazing being only one of those.

An extensive suite of scientific articles originating from the experiment at Hol have been published (an overwiev is available at http://folk.uio.no/atlemy/sauindeks.htm). Notably though, there has by now not been carried out any research specifically targeting a very important functional group, namely the pollinators. The preconditions at the experimental site, as well as the site-specific ecological knowledge base available, offered a unique opportunity to obtain new insights regarding grazing effects on alpine pollinator communities.

1.3 Sheep and their grazing habits

Sheep are now by far the most common grazer in Norwegian mountain fields; with a yearly presence of ~2.100.000 they constitute more than 50% of the total large herbivore biomass in these regions

(Austrheim *et al.*, 2011). The sheep variety used in the experiment at Hol is a modern synthetic breed (Norwegian whitesheep – Norsk kvit sau), which constitute ~90% of the total Norwegian sheep stock (source); it is a rather picky forager (source). Consequently, an experimental set-up with sheep grazing was the logical choice, and understanding the sheep's grazing ecology and how it varies in time and with scale, is important when predicting the ecological effects of its presence.

It has been common practice to order the sheep's grazing preferences as following: herbs > grass > sedges > heath/shrubs/trees (Nedkvitne *et al.*, 1995), but Mysterud & Austrheim (2005) makes it clear that this is a coarse approach, as much of the choice happens on a species level within and sometimes across (my addition) these groupings. Importantly, they show that grazing patterns (i.e. preferred vegetation types and plant choice) vary with sheep density, and Mobæk *et al.* (2009) show that preferred habitats are less selected at higher densities.

The initial research at Hol showed the following. The sheep did specifically forage on herbs as well as grasses and (most of the) shrubs in the genus *Salix*, but less on the important nectar plants in the genus *Vaccinium,* which had relative selection values of 0.3, *V. myrtillus; 0.2, V. uliginosum; and 0 V. vitis-idaea* (Mysterud & Austrheim, 2005). In addition, it is worth noting that herbs were eaten less as the season progressed, thus the diet shifted to include more of the less preferred plants; this was especially evident at grazing-increased treatment, indicating that herbs may be largely out-grazed at high grazing pressures. This tendency at high sheep densities not only affects sheer consumption volume, but also a shift in relative amounts of plants selected. Foraging on *Salix* spp. also declined as the season progressed, but in this case lower feed quality is likely the reason. However, Mysterud and Austrheim (2005) showed that there was no correlation between grazing treatment and the sheep's overall diet breadth.

The sheep's use of diferent vegetation types for grazing was not random, but differences were not significant between grazing treatments or throughout the season. The two *meadow* types were the most preferred habitats, followed by *snow-beds*, *marshes* and *dwarf shrub heath.* Use of the elevation gradient varied throughout the season and between years, as the vegetation develops differentially; the sheep tend to start out at low elevation levels but progress to graze at higher elevation during the middle of the season, where the plants are thought to be more nutritious at that time. At the grazing-

increased treatments, the sheep were found to stay at a lower elevation overall, indicating an inclination toward bulk feed at the more productive, lower areas.

1.4 <u>Vegetational responses to grazing</u>

It is crucial to distinguish among different temporal and spatial scales in understanding vegetational responses to grazing (Johnson, 1980; Senft *et al*., 1987; Wiens, 1989). Habitat productivity is also important in this regard, and complex interactions, e.g. between habitat, grazing damage, fertilizing and trampling, may lead to unpredictable outcomes (Jónsdóttir, 1991). At Hol, the interaction between elevation, vegetation type and grazing treatment has been shown to determine responses in plant community diversity at a medium time scale (Speed *et al*., 2013b). As the sheep at the experimental site are free to select vegetation type within their sub-enclosure, the relationship between vegetation type and grazing regime is complicated further. One can not then easily determine the specific grazing pressures that different vegetation types were subjected to across the elevational gradient. – These initial observations highlight the complexity of grazing interactions and the potential pitfall of making simplified assumptions.

Grazing intensity is always relative to primary production capacity, and while the different vegetation types vary in primary production capacity, there may also very well be local or regional differences within each category. Previous research suggest that habitat productivity decides floral diversity and whether grazing-resistant plants will come to dominate (Augustine & McNaughton, 1998; Austrheim & Eriksson, 2001). In highly productive habitats, plants can more easily compensate for losses to grazing, while highly selected herbs are less likely to persist in low productive areas (Bjor & Graffer, 1963). But at Hol, a high loss of diversity happened in the *tall forb meadow* vegatation type at the grazing-increased treatment. Following theory, this habitat of relatively high production capacity should be able to compensate fairly well for losses due to increased grazing pressure. However, it is likely that the mosaic structure of the experimental site makes this highly preferred vegetation type under the grazing-increased treatment subject to what is indeed a very high grazing pressure.

Short term effects on plant community composition following changes in grazing regimes are by nature very different from long term effects (Wiens, 1989). But plant community responses to different changes in grazing pressure may very well be temporally asymmetric, i.e. changes induced by

8

increased grazing pressure may materialize quicker than changes induced by decreased grazing pressure (Evju, 2009; Olofsson, 2006). Also, observable changes may play out differentially among vegetation types as time progresses. However, it can be useful to structure changes by the way they play out over different time scales, as in the following.

In a short time scale, grazing will change plant demographic processes, like aboveground biomass, plant survival and seed spread. Mysterud and Austrheim (2005) studied the effects of grazing on recruitment, survival and reproduction in two annual hemiparasitic herbs at Hol. They found lower recruitment of *Rhinanthus minor* (significant) and *Melampyrum sylvaticum* (almost significant) following the grazing-increased treatment when compared to either of the other treatments and seed production tended to be higher in the grazing-ceased treatment for both species.

On a medium time scale (~5-20 years), changes in plant community composition following different grazing regimes is by and large decided by the plants' competitive abilities and/or the grazing-selectivity of the herbivores, and how this interact with habitat productivity and environmental stress. Herbivores select plants with high nutrient contents and tend to avoid plants with traits conferring chemical or physical resistance to grazing. Decreased grazing pressure may favor strong competitors and lead to overall loss of diversity, while increased grazing pressure may induce a community change towards less palatable plants (Augustine & McNaughton, 1998; Mysterud & Mysterud, 1999), low/prostrate plants, plants with a high root-to-shoot ratio and plants with a certain regrowth capacity (Evju et al., 2009), and lead to a loss of diversity by the disappearance of highly selected herbs. But, there is also evidence that the most preferred plants continue to dominate or even increase their distribution (Augustine & McNaughton, 1998; Jónsdóttir, 1991; Bullock *et al*., 2001), while Evju *et al*. (2009) found no simple relationship between sheep selectivity and plant distributional responses to increased grazing pressure. Woody species (e.g. *Salix spp., Vaccinium spp.*) may increase in distribution with moderate grazing pressure, as competition with grasses and herbs is relaxed. But with high grazing pressure these may decrease as they are increasingly grazed (Wielgolaski, 1975; Speed *et al*. 2013a). Further, intermediate levels of disturbances may at this time scale decrease the abundance of dominant species, thus facilitating the persistence of rarer species by the process of competitive release (Winfree *et al*., 2007).

9

At a longer time scale, the entire ecosystem's dynamic may change following decreased and increased grazing regimes through plant succession taking a totally different path.

To understand grazing induced responses in plant diversity, it is also important to distinguish between spatial scales. At a local scale, grazing may increase (alpha) diversity through a continuous process of perturbation, but may lower spatial species turnover between nearby localities (beta diversity) through a homogenization process where plant communities conform to the grazing regime. A point to make a note of is that sheep may act as seed dispersal agents. At a regional scale, grazing is likewise thought to lower (gamma) diversity through the same homogenization process (Chaneton & Facelli, 1991; Olff & Ritchie, 1998). At Hol, no clear indications of homogenization has been found, although spatial species turnover increased in heathlands following the grazing-ceased treatment (Speed *et al*. 2013b).

Alpine plant communities in general are subject to rapid changes due to rising temperatures (Harsch et al. 2009), changes in mountain species richness have been linked to a warming climate (Pauli *et al*. 2012) and vegetation is displaced due to nitrogen deposition (Bassin *et al*. 2007). At Hol, these changes are most conspicuous by the upwards advancement of the tree line (Speed *et al*. 2010), but similar although more subtle changes apply to the alpine plant community in general, and this may vary with grazing regimes (Evju *et al*. 2009). For this reason, plant community changes due to climate change as well as major shifts in biogeochemical cycles and long transport pollution, cannot be confirmed unless changes in grazing regimes are first ruled out.

The grazing-maintained treatment has been effective in hampering the advancement of the (mountain birch) tree line at Hol (Speed *et al*., 2010, 2011, 2012), while the grazing-increased treatment has caused a downward shift in plant community composition of 4 m (Speed *et al*., 2012). Thus it is evident that grazing interact with environmental stress to lower the upper distribution of the plant community as a whole, see also Post and Pedersen (2008). Highly selected herbs like *Hieracium spp*., *Ranunculus acris* and *Geranium sylvaticum* have their maximum elevation shifted disproportionately downwards in the grazing-increased treatment and likewise upwards in grazing-ceased treatment.

Thus the research at Hol shows that to properly evaluate grazing effects, it is necessary to evaluate differential changes along the elevation gradient (Speed *et al*., 2013, Maurset, M. U., unpublished). The

following result reveals the danger of averaging effects over the elevation gradient: after 10 years of experiment at Hol, at the grazing-ceased treatment, diversity decreased by up to 3.7 species at low elevations, while it increased by up to 3.5 species at high elevations. Between 1150m and 1250m elevation there was little change. Interestingly Speed *et al.* (2013) point out that the upward shift in species diversity at Hol correspond to the upward advancement of the tree line (which at the grazing-ceased treatment stop at a maximum of 1200m elevation). As the diversity has been shown to decrease at a certain elevation as the tree line progress above it, this in effect means that the elevational level of maximum diversity will follow the ecotone, which is determined by the tree line.

The distribution of the shrubs in *Salix spp.* (which are key community shaping agents), is also determined by the interaction of grazing and elevation (Speed *et al.*, 2013). Though the upper distribution is limited by grazing, it responds positively to grazing at the lower elevations due to competitive release. thus contrasting the response shown by mountain birch.

The way grazing interacts with elevation implies that grazing management is a key determinant in shaping communities, with the potential to buffer climate-driven changes in plant communities as a whole. But the importance of primary production capacity and vegetation types has obvious implications for the transferability of conclusions drawn from the experiment at Hol and other grazing experiment.

1.5 Bumblebees

The relatively cold-adapted bumblebees (*Bombus* spp.*,* Latreille) are key pollinators of characteristic flowering plants in many boreal and alpine ecosystems. They are often numerous during peak flowering and can be relatively speciose even at high altitudes, making them ideal subjects for investigation.

Bumblebees are social nest-dwelling insects forming annual colonies with a high energy demand throughout the season. In the alpine parts of Southern Norway, the season is short but intense for these laboursome bees, as the climatic conditions demand. After bare patches appear in early summer, the queen bumblebee wake up from her underground beauty sleep. Hopefully for her, this event is synchronized with the early *Salix* spp. blooming. When her energy stores then are filled up, she starts

looking for a suitable nesting site, which will often be located in an abandoned rodents nest (Løken, 1973). A few weeks later, the first batch of worker bees will be on their wings to help their mother build up the colony, gathering resources in large part from the woody perennials in the genus *Vaccinium, e.g. V. myrtillus, V. uliginosum, V. vitis-idaea*, but for some of the larger alpine species, fabaceous plants might be the food of choice. Another batch or two of worker bees might still see the light of day, but already a couple of months after the queen first appears, the season is in decline (Løken, 1973) and the colonies fulfill their mission by giving birth to males and the queens of next year. As the season draws to an end, it might be composites that offer the most attractive nectar resources, e.g. *Leontodon* spp.*, Solidago virgaurea, Saussurea Alpina*, and maybe also a meeting place for these young romantics. After mating, the male has fulfilled its mission, and the queens must build up sufficient fat reserves before she dig herself down before the long winter.

Bumblebees gather nectar and pollen, and different species can be characterized as either doorstep foragers or long range foragers (Hellwig & Frankl, 2000). However, foraging range data does not exist for most species, but the foraging range of previously examined bumblebee species differ from 500 m up to several km (Goulson, 2010) and species with smaller individuals and/or smaller colonies tend to have shorter foraging ranges (Westphal *et al.*, 2006). Under some circumstances, alpine bumblebees may migrate downhill to draw resources from fruit blooming. While at other times lowland species might do the opposite to join in on the plentiful ericaceous blooming. When a bumblebee return to the nest aftter a succesful foraging trip, she can communicate this finding to her sisters who then use odor cues to search for the locality (Dornhaus, & Chittka, 1999, 2001).

Norway can be said to have a special responsibility for the bumblebees, housing 35 of the worlds ~ 250 species (Artsdatabanken, 2015a). Some of the alpine species, to which this study is concerned, has a big part of their (or even the main) world distribution in Norway (Discover Life, 2015). This responsibility is further outlined in a new and extensive report: *Climatic Risk and Distribution Atlas of European Bumblebees* (Rasmont *et al.*, 2015), which projects possible future geographical distributions for european bumblebees under different climate scenarios. The authors show that evident climatic changes are already causing problems for the bumblebees, but the projected future climate scenarios are really bad news; as much as 50% of the European bumblebee species are expected to go extinct under the most severe ("business as usual") scenario. Fennoscandia is suggested to serve as a last

refuge for those of the vulnerable southerly species that manage to migrate northwards. But as the climate heats up and tree lines continue to advance, the sturdy species already adapted to alpine conditions will have their ranges severely decreased as they become increasingly isolated towards mountain tops. On the other hand, vital populations are better equipped to withstand the negative impact of and adapt to the changing conditions (Williams *et al.,* 2007; Williams & Osborne 2009), thus making our stewardship a matter of prime importance.

1.6 <u>Aims</u>

Assumption: Differences in grazing pressure translate into differences in bumblebee abundance. through changes in plant communities or otherwise. Indirect and direct effects (source, Wilmer).

Aim:

1) *To assess whether and to what extent different levels of grazing pressure affect the abundance and diversity of an important group of pollinators, namely bumblebees*

Although the above was the main motivation, the comprehensive dataset is also informative in a more general way.

2. Method

2.1 <u>Data sampling</u>

Getting a sufficiently large amount of quality field data was a prime objective when choosing the method of observation. Transect walks have previously been shown to be an efficient way of monitoring pollinating insects (Westphal *et al.*, 2008), and was chosen despite terrain difficulties. Five 30m transects were placed in every sub-enclosure, making up a total of 45 transects; a total of 15 replicates for each experimental treatment. As a compromise between minimizing walking distance and placing the transects at random, I applied the following semi-random method for transect localisation.

As the contour lines around 1200m runs neatly along the hillside through all the sub-enclosures, I chose the 1160m contour line as a starting point. Then for each sub-enclosure, a straight imaginary line was drawn between the east- and west borders at the points intersecting with the 1160m contour line (if several points were located at 1160m, the southernmost point was selected). This line was then partitioned into 6 equal parts yielding five new helping points inside each sub-enclosure. From theses helping points the transects would then run along a straight line in a south to north direction, randomly

chosen between four options:

    a) 60m - 30m   south of the imaginary line (generally downhill)

    b) 30m -   0m   south of the imaginary line (generally downhill)

    c)   0m - 30m   north of the imaginary line (generally uphill)

    d) 30m - 60m   north of the imaginary line (generally uphill)

A set of pre-made rules excluded unfit transects, and if necessary I would reapply the randomization procedure on the remaining options. The rather short (30m) transect length originated from the need to keep the number of unfit transects at a reasonable level, and from a trade-off between number of transects and the time spent at each.

Transect exclusion rules:

    -20% or more of the transect length made up by a substrate that could never support flowers; like
      bare rock, snow or water.

    -The transect being judged unwalkable do to impenetrable vegetation, cliffs, crossing streams etc.

    -The transect leaving the sub-enclosure.

Elevation was measured for each transect (as the mean elevation calculated from the transect start and stop). All measurements including height, distance and direction were measured by GPS (Garmin GPSMAP 62s).

An infield weather station collected weather data., from which I include four variables in the statistical model: temperature, wind speed, relative air humidity and solar radiation. These measurements were available as averages on an hourly basis; thus a transect walk initiated at 12.34 would bring with it weather data averaged from measurements between 12.00 and 13.00.

A field assistant and I partitioned the transects between us such that he did all the transect walks in the ABC block, and half the DEF block, while I did the remaining half of the DEF block and all of the GHI block. The executive sequence of transect walks was a compromise between randomness of timing/order and between transect walking distance. The order of blocks, and then sub-enclosures within blocks, was randomised before each full turn (i.e. to be executed in a backwards nested manner).

14

Finally, transect walks within a sub-enclosure were allowed in any preferred order. As we in effect were two persons serving three blocks, one of us was allowed to start on the first block of a new full turn around the same time the other started the remaining block of the not yet completed full turn. We made sure that the DEF-block would not be occupied by both of us at the same time, by taking this into account in the randomization procedure. The transect walks were always conducted in a south to north direction and lasted around 2 minutes. The observer progressed steadily and added time when necessary for taking notes, netting insects etc. We registered any flower visiting insect 2m to either side and 2m forwards, and identified it to species or manageable taxonomic resolution, as well as which flower it visited when first observed. As the nature of the experiment did not specifically demand voucher specimens being taken, I instead opted to leave the system as undisturbed as possible for later research. This, I thought, would enhance the dataset, both in quality and quantity. Ethical reasons were also considered.

Over a ten day period from July 2. to July 11. 2014, we conducted as many transect walks as our feet could carry and weather conditions allowed; we were generally determined to avoid wasting energy on rainy days. Date and time of day was registered for each transect walk, as well as the identity of the observer.

2.3 <u>Statistical model</u>

I analysed the flower visitation rate of bumblebees (as seen as a whole) using the glmmADMB statistical package; a flexible mixed effect model environment (Fournier *et al*., 2012). – Count data theoretically belong to the Poisson statistical probability distribution, but the real time distribution of bumblebees is expectedly overly variable by nature, i.e. they form clusters by communicating or by other ecologically based causes. This is likely to result in over-dispersion when the Poisson distribution is applied to field data. Since this was not known in advance, I let the door open for the actual distribution of the observed data to guide which statistical probability distribution would be appropriate. – For model selection criterion, I chose BIC since it has been shown to be adequately conservative in a glmm model setting with many data points. This is because it maintains a more or less constant ratio between the likelihood and penalty for introduced covariates, while its counterpart AIC, likewise has turned out to be overly liberal. (Burnham & Anderson, 2002; Wagenmakers & Farrell,

15

2004).

In the model, the *transect walk* is the unit where observations took place, and *bumblebees* by flower visitation count is the *dependent variable*. I included the following *independent variables* in a full model search, with the BIC model selection criterion for calculating the most parsimonious model, ((r) indicates that the *independent variable* was tested as a *random effect*):
treatment , *block* (r) , *sub-enclosure* (r) , *transect* (r) , *observer* (r) , *day* (r) , *day number* , *time of day* (standardised and sine transformed) , *time of day* (standardised and cosine transformed) , *temperature* , *wind speed* , *relative air humidity* , *solar radiation* , *elevation*.

Time of day was standardised so that a full 24 hour day was represented by the *unit circle* (i.e. from 0 to 2π). It was then separated into two independent *independent variables*, of which one were sine- and the other cosine transformed to represent naturally occurring daily fluctuations; the two functions reaching their extrema (minima/maxima) at 6.00/18.00 and 0.00/12.00 respectively, in order to complement each other.

The following independent variables were tested as add-ons to the "best model" from the initial full model search. These were conservatively selected *apriori* for their presumable ecological meaningfulness in order to avoid data dredging, and tested in a stepwise forward selection procedure:

Interaction terms:
    temperature : *wind speed* , *treatment* : *elevation*.

Second order polynomial effects (each variable tested with its extremum *apriori* set at the arithmetic mean):
    temperature^2 , *air humidity^2* , *solar radiation^2* , *day number^2*.

After the stepwise forward selection procedure, I used the new and conclusive "best model" as a starting point, from where I went on to include the *treatment* variable in a new model for comparative purposes only, i.e. to examine how the experimental treatments related to one another. Statistical analyses were carried out in the R statistical environment (R Development Core Team, 2013).

16

3. Results

A total of 6 transects were deemed unfit and excluded. The distribution of transects, evenly spaced along the hillside of the patchy landscape, seemed to capture the variation in vegetation types quite well for each sub-enclosure, although this was not measured. Transect elevation ranged from 1138m – 1200m with a mean of 1169m.

Over a ten day period from July 2. to July 11., we conducted as many transect walks as our feet could carry and the weather conditions allowed. In a given day, and under good conditions, we managed two full turns, i.e. every transect was walked twice. On July 6. and 7. we did not carry out any walks due to considerable rainfall, while on July 11. we finished after one full turn. Thus we completed 15 turns, giving a total of 45 transects x 15 walks = 675 transect walks.

Table 1. sum up the essentials of the measurements from the weather station as coupled to the transect walks.

Table 1. Measurements from the weather station.

	unit of measurement	mean	min	max
temperature	degrees celcius	14.5	6.6	21.5
wind speed	m/s	2.75	0	5.7
relative air humidity	percent	56.7	34.3	99.7
solar radiation	W/m^2	462.7	19	862

When seeing all bumblebees as a whole, a total of 649 flower visits were recorded on the 625 x 30m transect walks, thus we on average had to walk 28.9m to encounter one specimen. The grazing-maintained treatment came out on top with 260 observations, followed by the grazing-ceased treatment with 223 observations and lastly the grazing-increased treatment with 166 observations. These results will be treated more thoroughly in the statistical model.

Variation in insect distribution will in the following be expressed as CV = standard deviation/mean, which is a useful statistical measure of dispersion for comparing units with different means. However, conclusions drawn from the CV measure should be treated cautiously. – It can be useful to identify five levels of measurement, each represented by a unit, which are here ordered hierarchically from bottom to top:

(1) *transect walk* , (2) *transect* , (3) *sub-enclosure* , (4) *treatment* , (5) *all observations combined*.

17

(Block is a possible unit as well and equivalent to treatment in level, but is not considered further here.) Variation in one level can be measured at any of the levels below it in the hierarchy. The following examples may clarify.

Variation in *all observations combined* can be measured at the *sub-enclosure* level:

the 9 sub-enclosure totals ranged from 27 to 126 flower visits, with a mean of 72.1. The CV is 0.43

Variation in *all observations combined* can be measured at the *transect* level:

the 45 transect totals ranged from 0 to 69 flower visits, with a mean of 14.4. The CV is 0.95.

Variation in *all observations combined* can be measured at the *transect walk* level:

the 625 transect walks ranged from 0 to 15 flower visits, with a mean of 0.96. The CV is 1.62.

While the data-set is based on count data, as we move up in levels (and thus number of observations) the distribution approaches the normal statistical distribution due to the central limit theorem. – The distribution of bumblebee observations as a whole is summed up in table 2.

Table 2. Variation in frequency of flower visiting bumblebees, compared at different levels of measurement. CV=coefficient of variation. Blue: all observations combined; variation is shown by three different levels. White colour=grazing-ceased. Pink colour=grazing-maintained. Red color=grazing-increased.

unit	variation by	instances	sum	mean	min	max	CV
all observations combined	sub-enclosures	9	649	72.1	27	126	0.43
all observations combined	transects	45	649	14.4	0	69	0.95
all observations combined	transect walks	675	649	0.96	0	15	1.62
Treatment = Grazing-ceased	transects	15	223	14.9	0	69	1.2
Treatment = Grazing-maintained	transects	15	260	17.3	3	36	0.67
Treatment = Grazing-increased	transects	15	166	11.1	0	36	0.97
Sub-enclosure A	transects	5	126	25.2	6	69	1.09
Sub-enclosure B	transects	5	79	15.8	0	36	1.04
Sub-enclosure C	transects	5	94	18.8	3	36	0.79
Sub-enclosure D	transects	5	92	18.4	11	31	0.51
Sub-enclosure E	transects	5	32	6.4	3	14	0.74
Sub-enclosure F	transects	5	60	12	4	18	0.61
Sub-enclosure G	transects	5	65	13	0	24	0.77
Sub-enclosure H	transects	5	27	5.4	0	9	0.66
Sub-enclosure I	transects	5	74	14.8	6	36	0.82

As we recorded bumblebees to species if possible or otherwise species groups, a total of seven such

taxonomic entities were found tenable to represent the present bumblebee fauna and recorded. A more detailed overview of bumblebee distribution is available in the appendix. For other insects, the managable groupings were small flies, vespid wasps, syrphid flies and butterflies. We observed no other flower visiting insect taxa.

All obseved flower visiting flies were small and grey-black in appearance, they were recorded 488 times; sub-enclosure observation rate ranged from 1 to 200, with an average of 54.2. Vespid wasps were recorded 25 times; sub-enclosure visitation rate ranged from 0 to 8. Syrphid flies were recorded 12 times; sub-enclosure visitation rate ranged from 0 to 2. Butterflies showed up with only one flower visit. The distribution of insect taxon observations and the accompanying flowers visited is summed up in table 3.

Table 3. Flower visiting insects by taxon. Blue: insect taxon totals. Magenta: insect taxon variation by sub-enclosures. Green: insect taxon totals partitioned between flower taxa visited. Yellow: emphasises the bumblebee total. B.=*Bombus*, gr.=group, sub.=sub-enclosure, CV=coefficient of variation, Sal=*Salix* spp., V.myr=*Vaccinium myrtillys*, V.uli=*Vaccinium uliginosum*, V.vit=*Vaccinium vitis-idaea*, G.syl=*Geranium slvaticum*, S.dio=*Silene dioica*, P.cae=*Phyllodoce caerulea*, A.pol=*Andromeda polifolia*, Mel.=*Melampyrum spp.*, R.acr=*Ranunculus acris*, P.ere=*Potentilla erecta*, Vio.=*Viola spp.*, R.cha=*Rubus chamaemorus*, T.eur=*Trientalis europaea*, Tar.=*Taraxacum spp.*, Hie.=*Hieracium spp.*, NA=flower unidentified

| | total | By sub-enclosures | | | | By flower taxa visited | | | | | | | | | | | | | | | | |
insect taxon	sum	mean	min	max	CV	Sal.	V.myr	V.uli	V.vit	G.syl	P.cae	Mel.	S.dio	A.pol	R.acr	P.ere	Vio.	R.cha	T.eur	Tar.	Hie.	NA
B. jonellus	130	14.4	3	31	0.58	30	28	41	27	1	1	0	1	0	0	0	0	0	0	0	0	1
B. lapponicus gr.	273	30.3	7	68	0.57	62	71	106	27	5	1	0	1	0	0	0	0	0	0	0	0	0
B. pratorum	102	11.3	4	19	0.54	45	18	19	12	6	0	2	0	0	0	0	0	0	0	0	0	0
B. balteatus	6	0.7	0	2	1.28	1	0	2	1	1	0	0	0	1	0	0	0	0	0	0	0	0
B. polaris	29	3.2	0	10	1.16	4	8	14	2	0	0	0	0	0	0	0	0	0	0	0	0	1
B. wurfleini	2	0.2	0	1	–	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
B. lucorum gr.	2	0.2	0	1	–	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Unknown B.	105	–	–	–	–	44	32	15	7	5	2	0	0	0	0	0	0	0	0	0	0	0
Bombus total	649	72.1	27	126	0.43	187	157	197	78	19	4	2	2	1	0	0	0	0	0	0	0	2
Small flies	488	54.2	1	200	1.45	23	0	0	0	144	0	0	0	0	267	46	2	2	1	2	1	0
Syrphid flies	12	1.3	0	2	0.69	5	2	0	0	0	0	0	0	0	0	4	0	0	1	0	0	0
Vespid wasps	25	2.8	0	8	0.99	8	14	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Butterflies	1	0.1	0	1	–	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

For the statistical model, the variable nature of the observations proved the Poisson statistical distribution unsuitable, due to severe over-dispersion. However, the negative binomial distribution proved better equipped to represent the actual data distribution; a comparative test confirmed that the observed data were 10^3 times less unlikely under the latter distribution, which was then favoured for the model.

The full model search yielded the following "best model":

bumblebees ~ day number + time of day (cosine transformed) + *transect* (r)

The stepwise forward selection procedure added one additional independent variable, *solar radiation²* (solar radiation as a second order polynomial function), to the existing best model. Conclusively, bumblebee distribution could best be explained by this model setting as:

bumblebees ~ day number + time of day (cosine transformed) + *transect* (r) + *solar radiation²* (as a second order polynomial function).

Summary of the conclusive "best model" is shown in figure 2.

```
Call:
glmmadmb(formula = bumblebees ~ (1 | transect) + day_number + I(cos(2 *
  pi * time)) + solar_radiation2, data = tab, family = "nbinom")

AIC: 1669.7

Coefficients:
                      Estimate  Std. Error  z value  Pr(>|z|)
(Intercept)          -7.76e-01    2.96e-01    -2.62   0.00874 **
day_number           -5.55e-02    1.69e-02    -3.27   0.00106 **
I(cos(2 * pi * time))  -1.02e+00    2.85e-01    -3.57   0.00036 ***
solar_radiation2     -2.66e-06    8.68e-07    -3.06   0.00219 **
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Number of observations: total=675, transect=45
Random effect variance(s):
Group=transect
           Variance    StdDev
(Intercept)    0.8198    0.9055

Negative binomial dispersion parameter: 2.6668 (std. err.: 0.57582)

Log-likelihood: -828.831
```

Figure 2. Model summary of the conclusive "best model". The expected values are calculated as: f(x1,x2,x3)=exp(b0+b1*x1+b2*x2+b3*x3), where the values of "b0", "b1", "b2" and "b3" comes from the model output "Esitmate".

A model-based interpretation of the observed data indicate:

-a declining linear response to *day number* as the field work period progress.

-a cosine shaped response to *time of day* with the maximum around 12.00. (This time was set

apriori, but inclusion in the "best model" indicates that 12.00 lies within the estimated

confidence interval of the true maximum.)

-that *transect* (r), by the property of "being variable by nature", confer a significant amount of heterogeneity to the data that cannot be explained by the other independent variables.

-a second order polynomial response to *solar radiation* with the maximum around its mean.

Figure 3 (a, b and c) show trajectories representing the magnitude of effects (on bumblebee flower visitation rate) as imparted by the three BIC-selected *fixed effect – independent variables*. The trajectories are calculated as relative responses in bumblebee flower visitation rate to changing conditions. Responses are shown relative to data-set maxima, which are given an arbitrary response value of 1. NB! These figures are only meant as a visualisation of the model output, and must be treated as such. I.e. these are isolated effects where the other variables are fixed and possible correlations are neglected – further no attempts were made to find the true maxima of each response variable – as well as other obstacles of model to true ecological response interpretation).
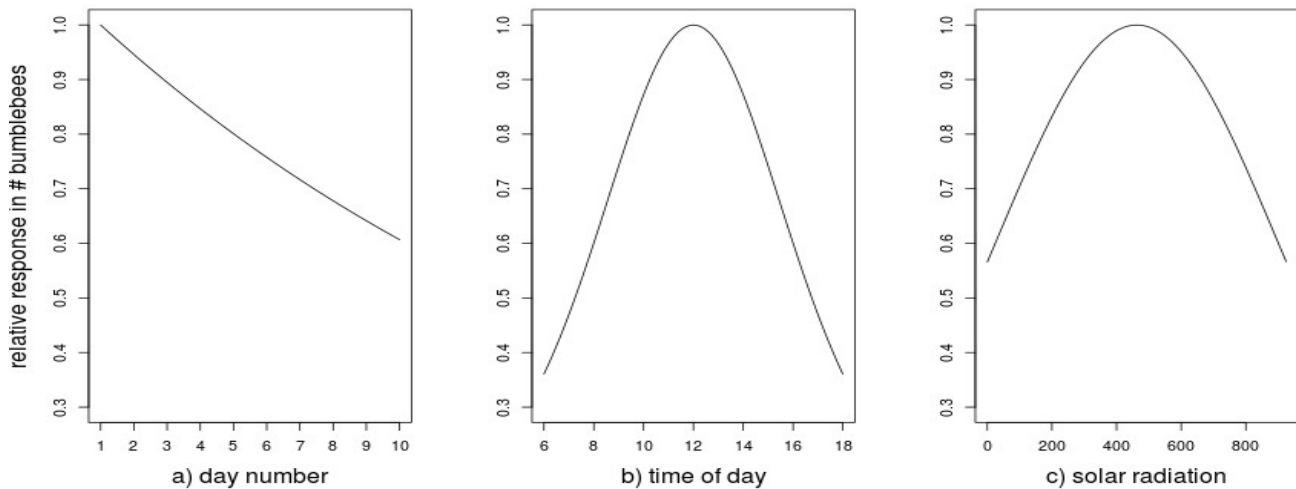

Figure 3. Trends in the three *fixed effect – independent variables* included in the conclusive "best model", with trajectories representing the magnitude of effects these impart on bumblebee flower visitation rate. Responses are shown relative to data-set maxima, which here have been given an arbitrary response value of 1 : a) day number, b) time of day, c) solar radiation. NB! This figure is based on many assumptions that in sum may diverge significantly from reality, and must thus not be over-interpreted.

As already evident, *treatment* is not included in the best model, and thus responses in bumblebee flower visitation rate to grazing treatments in-between, are not significant. Figure 4a show *treatment* plotted by baseline date; visualised by quantiles, 95% confidence intervals and outliers. This is an OK starting point, but a rather poor representation as a tool for in-depth exploration. However, after forcing

the inclusion of *treatment* in a new model, the model output is now corrected for other model parameters. Figure 4b will help explore how the grazing treatments relate to each other by visualising how the grazing-ceased and grazing-increased treatments, represented by the two boxes which show the expected response values (thick line) with 95% confidence intervals (lower and upper borders), relate to the grazing-maintained treatment, whose expected value is represented by the line at 1.0 in the response axis.
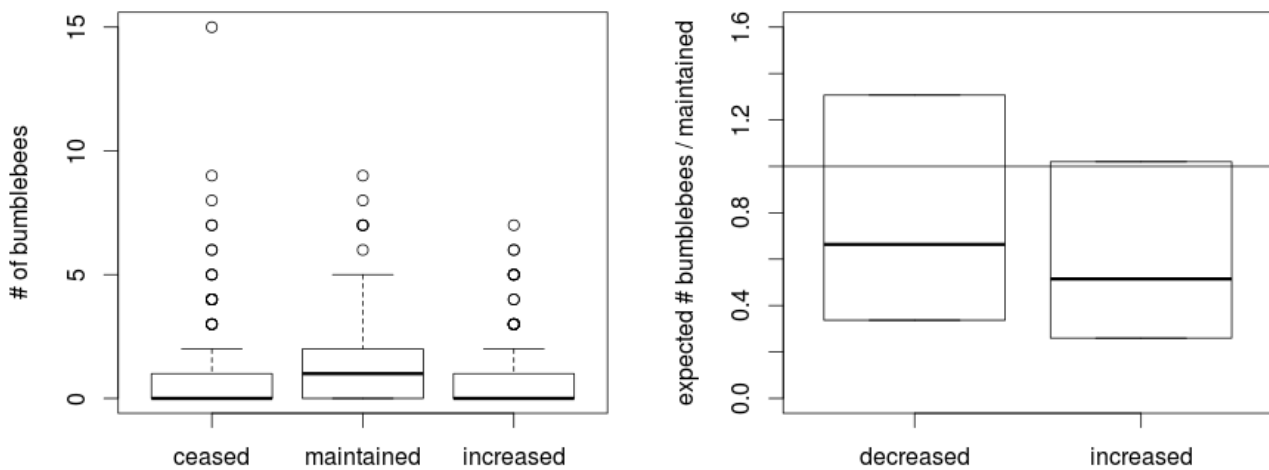

Figure 4. a) Grazing treatments are plotted by baseline data. Quantiles, 95% confidence intervals and outliers are shown. b) The grazing-ceased and grazing-increased treatments are represented by the two boxes, which show expected response values relative to the grazing-maintained treatment, whose expected value is represented by the line at 1.0.

4. Discussion

Initial experimental issues

Although I am generally happy with the experiment as a whole, I will go straigth to the issues. First of all, I now understand that even the moderate elevational gradient at Hol, and its interaction with grazing treatment is more influential on the plant communities and interactions than I first imagined. Even though my transects spanned from 1138m to 1200m, this was not sufficient and I do regret not taking the elevation gradient as such into the study design. This however, would have had to be weighed up against the cost of increased walking and less data.

The second point is the now understood influence of well defined vegetation types or vegetation main types (e.g. *meadows, snow-beds*) on bumblebee appearances, as sheep grazing does not change these over a medium time scale. This should either have been sorted out in advance, by assigning transects to different vegetation types intentionally, or by measuring the relative amounts of each transect belonging to which vegetation type, for inclusion in the model. Then possible interactions between grazing pressure and vegetation type could also have been sorted out. When that is said, the only vegetation type that gave really poor flower counts was *lichen heath*; two of the transects were almost exclusively in this vegetation type but I believe it's presence did not change the outcome dramatically.

It must also be said why I decided not to count flowers in the transects; this was due to the fact that flowers of *Vaccinium* spp. are inherently difficult to count and the fact that if analysed in a regular way they would likely correlate with grazing treatment but with a stronger effect on bumblebee flower visitation rate, thus masking the most interesting independent variable. Also, information on grazing effects on plant communities at Hol is available elsewhere.

Limitations to interpretation
As the foraging range of previously examined bumblebee species differ from 500 m up to several km, a bumblebee seen visiting a flower might still have its home in another sub-enclosure, or utilize resources from several sub-enclosures during a trip or throughout the season. This means that treatments cannot be seen as overall independent of one another, and my findings must be regarded merely as an estimate of the preferred foraging habitats at the time. However, in alpine habitats, the season is short and colonies are therefore expectedly small. Nevertheless, it seems likely that most species regularly fly more than the few hundred meters needed to cross from one sub-enclosure into another. Also, as a note of importance, there seems to be no clear tendency for the bumblebees to forage close to the nest compared to further away (Dramstad *et al.,* 2003).

However, the grazing treatments whose bumblebee population at certain times is the most negatively affected by grazing (or absence of such), could arguably profit from adjoining areas with better conditions, as negative impacts from inbreeding and local extinctions are non existent. This could be so due to the selective sheep grazing habits coupled with the bumblebees need for a continuous supply of

23

pollen and nectar to reproduce; thus if a sub-enclosure lacks key plants at certain times, this could be compensated for by looking elsewhere. Reinforcing this argument, the key plants flowering at the time of the research were among the less popular sheep forage, while later on, conditions might very well get worse at the grazing-increased treatment due to high selectivity on composites (Kausrud *et al.*, 2005)

Nesting or egg-laying sites are necessary for insects to fulfill their life cycle, the specific need for which will vary widely between taxa. In addition to the damage grazing and trampling does to the flower resources on which the pollinators depend, nesting sites might also get destroyed by trampling. The relative effect of this at Hol is hard to judge, but the natural patchy distribution of resources in the otherwise low productive landscape and relative moderate size of sheep makes it unlikely to be an important factor even at high grazing intensity. As a curiosity, bumblebees might get negatively affected by high grazing pressures indirectly, as this means less mice due to increased competition for resources (Mysterud & Austrheim, 2005).

Alpine pollinator communities

Arctic and northern hemisphere alpine pollinator communities are made up in large part by "muscoid flies", "smaller flies" and bumblebees (Totland, 1994, 2001, this study). Some more exotic flower visitors are: *Vespidae* which can be very numerous at times as seen on *Saxifraga aizoides* (personal observation, Jotunheimen 2014) but their pollination efficacy is largely unknown; *Parasitica*; *Syrphidae; and Lepidoptera*. A few sturdy species of solitary bees (e.g. *Andrena lapponica*, *Lasioglossum boreale, Osmia laticeps*) can also present in the alpine regions of Southern Norway, although not very numerous.

Bumblebees and flies turned out to be the two dominant groups in this data-set, however, the flower preferences of these are almost non-overlapping, thus supporting two distinct and important pollination networks with few links in-between, but *Salix* spp. being a nexus. As a pilot study in 2013 confirmed, bumblebees are dominating visitors to many of the characteristic alpine plants, thus the main focus of this research was decided in advance to be bumblebees. The fact that flower visitation by flies was much more variable than by bumblebee can bee interpreted by the spread of flowers or flies lower tolerance; althoug it might be that flies are highly affected by selective grazing on favourite, e.g

Ranunculus acris, Geranium sylvaticum.

When it comes to bumblebee species, it must first be noted that as we captured no specimens, the following results must be treated as the uncertain field observations they are. Nevertheless, they should give a good indication of the species diversity in the experimental field area and the different sub-enclosures. About one in six observed bumblebees were not identified to species on the fly, and is treated as unknown bumblebee observations. The *B. lapponicus* group consists of this and *B. monticola*; only recently is it generally recognised that these atually constitute two species, and they are practically indistinguishable save for molecular methods where they co-occur in Southern Norway. They are very closely related as well (Cameron *et al*. 2007). *Bombus alpinus* is another not so easy species that can sometimes be confused with *B. polaris*, particularly worn out individuals. The often large workers can be confused with the *B. lapponicus* group queens. The *B. lucorum* group consists of this and *B. cryptarum* and *B. magnus*, and sometimes *B. terrestris* workers will be very similar as well. They are also notoriously hard to identify. Previous work suggest that *B. cryptarum* is the most likely inhabitant of the lower alpine zone.

Three bumblebee species/species-groupings stood out in the flower visitation count. These, which all belong to the small and lively bees in the *Pyrobombus* subgenus (Williams *et al*. 2008), all have quite wide habitat ranges and are common inhabitors of norwegian mountains and heathland; they were *B. lapponicus* gr. (273 visits), *B. jonellus* (130 visits) and *B. pratorum* (102 visits). Of these, the two former are short tongued and show a strong preference for ericaceous plant (in addition to *Salix*), *while B. pratorum* is a medium tongued species with a somewhat wider foraging range, although this is not very evident in the data, but notably the two only visits of *Melampyrum* spp. was made by this species. Next came the bigger bees in the *Alpinobombus* subgenus (Williams *et al*. 2008): *B. polaris* (29 visits) and *B. balteatus* (6 visits). The presence of the related *B. alpinus* could not be confirmed, though it is not impossible that a few individuals was recorded as one of the two above-mentioned species to be mistaken for. These *Alpinobombus* species have medium tongue length and a wide foraging range, but are said to show a preference for *Fabaceae* herbs, e.g. *Astragalus alpinus* and *Oxytropis lapponica*, which were conspicuous in their absence in the transects, and only few are found in the experimental field overall. Although *Alpinobombus* naturally occur in lower numbers than *Pyrobombus*, this observation might further explain their considerably lower presence. *B. wurfleini* (2 visits) and *B.*

lucorum group (2 visits) rounded it all off. In addition, the social parasite *Bombus flavidus* was observed outside the transects. Thus, a total of at least eight bumblebee species were found inside the experimental field area

Timing of the study

2014 was a warm, but not too dry, summer in Southern Norway, yielding good conditions for most insects. The two rainy days in the middle of the otherwise warm and precipitation free sampling period reflect this. One observed flower visiting bumblebee per 28.9m transect walked, was a very high rate compared to the pilot study in 2013 when I observed one flower visiting bumblebee per 194.6m. Although not directly comparable due to slightly different sampling dates (seasonal dependency) and weather conditions during the sampling period, this observation still underscores the highly variable nature of alpine insect population abundances.

The relatively short duration of the sampling period (10 days) can in part be justified by Hegland et al. (2010), who showed that even if monitoring is limited to a relatively short time span at peak flowering dates, relatively little information will be lost in constructing (full seasonal) pollination networks. Also, bumblebees are resource demanding insects and for a colony to succeed it must likely be very active during peak flowering of the important nectar plants in *Vaccinium* spp.

On the other hand, plants that offer important pollen and nectar resources at the beginning or end of the season, might be affected by grazing in contrasting ways (Mysterud & Austrheim 2005) , and this is further affected by the timing of release and re-capture of livestock, events which accordingly can be used to modify grazing effects relative to different plants. An extended sampling period could be interesting to apply for long lived pollinator entities like bumblebee colonies in a grazing-experimental setting. Further, to me its not known any research on the interaction between seasonality, flower abundance and grazing as limiting factors for bumblebees in alpine ecosystems; this could be an interesting research topic by itself and would yield valuable insights.

Maurset, M.U. (unpublished) did her master thesis (2015) on plan responses to grazing along the gradiane. In her research, Vaccinium myrtillus and Geranium sylvaticum responded negatively to increased grazing but not to elevation. While for *V. uliginosum* and *V. vitis-idaea*, grazing had no effect, while they seemed to have an upward shift overall. For Salix spp. she did not find any effect of either grazing treatment nor elevation. Based on existing plant data, however, it is not easy to predict the effects of grazing on bumblebee abundances at medium elevations, save for the increased grazing treatmen which might be considered the least attractive. At lower elevations though, increased grazing might do better overall, while the opposite might be true for higher elevations. For decreased grazing the effects are likely opposite increased grazing as research on plant community responses have revealed.

In sum, moderate grazing pressure has been shown to suppress the generally unwanted elevational advance of plant communities (the tree line most importantly), and might even contribute to increased biodiversity at the medium range elevations by the process of competitive release, while at the same time avoiding the most adverse effects caused by high grazing pressures on highly selected herbs. Thus there does exist a point along the grazing disturbance gradient between none and high grazing pressures that is optimal with regard to maintaining high diversity in, and the distinctiveness of, the mountaneous heathlands. Likewise, the results from this study indicate an optimum-point in bumblebee abundance at somewhat medium levels of grazing pressure. Further, as pollinators and flowers are mutualists, it follows that the optimum for each part in the mutualism will attract the other. Thus in sum we find that moderate grazing at least can not be dis-recommended regarding effects on bumblebees populations.

5. Conclusion

This study confirm that bumblebee foraging patterns are indeed variable by nature, making it hard to draw conclusions with certainty, even from relatively fair sized data-sets like this one. Despite of that, knowledge from this study can be combined with the results from plant community response studies at Hol in a fruitful way. – The overall dominant role of bumblebees underlines that maintaining robust bumblebee populations are important for seed set in key heathland plants, while this in turn play back

at the pollinator assemblages in a positive feedback loop. Thus plant and pollinator communities assist each other by each cushioning negative warming influences on the other; robust bumblebee populations are better equipped to withstand these, while failing seed set in key alpine plants likewise will lead to a loss of plant diversity. Grazing will contribute to this common cause by supressing the elevational advance of the tree line, but only up to a certain level of grazing pressure. As both plant and bumblebee communities independently can be said to show an optimal response to moderate levels of grazing, their mutualistic relationship and the law of attraction makes it more likely that this optimum is soundly located at a moderate level of grazing pressure.

The results of the ongoing research at Hol is highly interesting because it can tell us how to best administer this and similar resources in a long term perspective, when taking into account both the needs for livestock production, biodiversity maintenance as well as other interests. As no work had previously been carried out on pollinator assemblages at Hol, the results from this study supplement the existing suite of research, and contribute positively to the whole of the ecosystem understanding.

6. References

Artsdatabanken. (2015). *Humler på nett*. Retrieved June 1, 2015, from
    http://data.artsdatabanken.no/pages/160179
Artsdatabanken. (2015). *Norges villbier på nett*. Retrieved June 1, 2015, from
    http://www.artsdatabanken.no/Article/Article/133991
Augustine, D. J. & McNaughton, S. J. (1998). Ungulate effects on the functional species composition
    of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management*,
    62, 1165–1183.
Austrheim, G., & Eriksson, O. (2001). Plant species diversity and grazing in the Scandinavian
    mountains - patterns and processes at different spatial scales. *Ecography*, 24, 683–695.
Bassin, S., Volk, M., Suter, M., Buchmann, N., & Fuhrer, J. (2007). Nitrogen deposition but not ozone
    affects productivity and community composition of subalpine grassland after 3 yr of treatment.
    New Phytologist, *175*(3), 523-534.
Bjor, K., & Graffer, H., (1963). Beiteundersøkelser på skogsmark. Forskning og forsøk i landbruket
    14:121-365.
Bullock, J. M., Franklin, J., Stevenson, M. J., Silvertown, J., Coulson, S. J., Gregory, S. J., & Tofts, R.
    (2001). A plant trait analysis of responses to grazing in a long-term experiment. *Journal of Applied
    Ecology*, 38:253–267
Burnham, K. P., & Anderson. D. R. (2002) Model selection and multimodel inference: a practical
    information-theoretic approach, 2nd edn. New York: Springer.
Cameron, S. A., Hines, H. M., & Williams, P. H. (2007). A comprehensive phylogeny of the bumble
    bees (Bombus). *Biological Journal of the Linnean Society*, *91*(1), 161-188.
Chaneton, E. J. & Facelli, J. M. (1991). Disturbance effects on plant community diversity: spatial

scales and dominance hierarchies. *Vegetatio*, 93, 143–155.

Discover Life. (2015). *Bombus.* Retrieved June 1, 2015, from e.g.:
http://www.discoverlife.org/mp/20q?search=Bombus
http://www.discoverlife.org/mp/20m?kind=Bombus+alpinus

Dornhaus, A., & Chittka, L. (1999). Insect behaviour: Evolutionary origins of bee dances. *Nature*, *401*(6748), 38-38.

Dornhaus, A., & Chittka, L. (2001). Food alert in bumblebees (Bombus terrestris): possible mechanisms and evolutionary implications. *Behavioral Ecology and Sociobiology*, *50*(6), 570-576.

Direktoratet for naturforvaltning (1995). *Inngrepsfrie naturområder i norge*. Registrert med bakgrunn i avstand fra tyngre tekniske inngrep. DN-rapport, 6-1995.

Dramstad, W. E., Fry, G. L., & Schaffer, M. J. (2003). Bumblebee foraging—is closer really better?. *Agriculture, ecosystems & environment*, *95*(1), 349-357.

Evju, M., Austrheim, G., Halvorsen, R., & Mysterud, A., (2009). Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. *Oecologia*, 161: 77–85.

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., ... & Sibert, J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, *27*(2), 233-249.

Goulson, D. (2010). *Bumblebees: behaviour, ecology, and conservation* (No. Ed. 2). Oxford University Press.

Harsch, M. A., Hulme, P. E., McGlone, M. S., & Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12, 1040–1049.

Hegland, S. J., Dunne, J., Nielsen, A., & Memmott, J. (2010). How to monitor ecological communities cost-efficiently: The example of plant–pollinator networks. *Biological Conservation*, *143*(9), 2092-2101.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.

Jónsdóttir, I. S. (1991). Effects of grazing on tiller size and population dynamics in a clonal sedge (Carex bigelowii). *Oikos*, 62:177-188.

Kausrud, K., Mysterud, A., Rekdal, Y., Holand, Ø., & Austrheim, G. (2006). Density-dependent foraging behaviour of sheep on alpine pastures: effects of scale. *Journal of Zoology*, *270*(1), 63-71.

Körner, C. (2003). *Alpine plant life: functional plant ecology of high mountain ecosystems*; with 47 tables. Springer Science & Business Media.

Kvamme, M. (1988). Pollen analytical studies of mountain summer farming in Western Norway. In: Birks, H. H., Birks, H. J. B., Kaland, P. E., Moe, D. (eds). The Cultural landscape, past, present and future. *Cambridge University Press*, Cambridge, pp 349-367.

Kålås, J.A., Viken, Å., Henriksen, S., & Skjelseth, S. (red.), (2010). Norsk Rødliste for arter 2010. Artsdatabanken, Norge. 480 s.

Løken, A. (1973). *Studies on Scandinavian bumble bees (Hymenoptera, Apidae)*. Universitetsforlaget.

Moe, D., Indrelid, S., Fasteland, A. (1988). The Halne area, Hardangervidda. Use of a high mountain area during 5000 years - an interdisciplinary case study. In: Birks, H. H., Birks, H. J. B., Kaland, P. E., Moe, D. (eds). The Cultural landscape, past, present and future. *Cambridge University Press*, Cambridge, pp 429-444.

Mysterud, A., & Austrheim, G. (2005). Ecological effects of sheep grazing in alpine habitats. Shortterm effects. *Utmarksnæring i Norge* 1-05, 1–91.

Mobæk, R., Mysterud, A., Loe, L. E., Holand, O., & Austrheim, G. (2009). Density dependent and temporal variability in habitat selection by a large herbivore; an experimental approach. *Oikos*, 118, 209–218.

Mysterud, A., & Mysterud, I. (1999). Bærekraftig bruk og forvaltning av Setesdals Vesthei og Ryfylkeheiene. En utredning med spesiell vekt på økologiske effekter av husdyrbeiting i utmark. Utmarksnæring i Norge 1-99:1-197.

Mysterud, A., & Austrheim, G. (2005). Økologiske effekter av sauebeiting i høyfjellet: korttids-effekter. *Utmarksnæring i Norge*, *1*, 1-91.

Nedkvitne, J. J., Garmo, T. H., Staaland, H. (1995). Beitedyr i kulturlandskapet. Landbruksforlaget, Oslo.

Olff, H. & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution*, 13, 261–265.

Olofsson, J. (2006). Short- and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. *Journal of Ecology*, 94, 431–440.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B. *et al*. (2012) Recent plant diversity changes on Europe's mountain summits. *Science*, 336, 353–355.

Post, E., & Pedersen, C. (2008). Opposing plant community responses to warming with and without herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 12353–12358.

R Development Core Team (2013). R: a language and environment for statistical computing. *R foundation for statistical computing*, Vienna, Austria.

Rekdal, Y., (2001). Vegetasjon og beite ved Minnestølen, NIJOS-dokument, 23-01, 1-21.

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2010). Experimental evidence for herbivore limitation of the treeline. *Ecology*, 91, 3414-3420.

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2011). Growth limitation of mountain birch caused by sheep browsing at the altitudinal treeline. *Forest Ecology and Management*, 261, 1344-1352.

Speed, J. D. M., Austrheim, G., Hester, A. J., & Mysterud, A. (2012). Elevational advance of alpine plant communities is buffered by herbivory. *Journal of Vegetation Science*, 23:617-625.

Speed, J. D. M., Austrheim, G., Hester, A. J. & Mysterud, A. (2013). The response of alpine Salix shrubs to long-term browsing varies with elevation and herbivore density. *Arctic Antarctic and Alpine Research*, 45: 584-593.

Speed, J. D. M., Austrheim, G., & Mysterud, A. (2013b). The response of plant diversity to grazing varies along an elevational gradient. *Journal of Ecology*, 101: 1225-1236.

Totland, Ø. (1994). Influence of climate, time of day and season, and flower density on insect flower visitation in alpine Norway. *Arctic and Alpine Research*, 66-71.

Totland, Ø., & Sottocornola, M. (2001). Pollen limitation of reproductive success in two sympatric alpine willows (Salicaceae) with contrasting pollination strategies. *American Journal of Botany*, *88*(6), 1011-1015.

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., ... & Steffan-Dewenter, I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, *78*(4), 653-671.

Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychon Bull Rev* 11: 192–196.

Walther-Hellwig, K., & Frankl, R. (2000). Foraging distances of Bombus muscorum, Bombus lapidarius, and Bombus terrestris (Hymenoptera, Apidae). *Journal of Insect Behavior*, *13*(2), 239-246.

Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2006). Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia*, *149*(2), 289-300.

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional Ecology*, 3:385-397.

Williams, P. H., Araújo, M. B., & Rasmont, P. (2007). Can vulnerability among British bumblebee (Bombus) species be explained by niche position and breadth?. *Biological Conservation*, *138*(3), 493-505.

Williams, P. H., Cameron, S. A., Hines, H. M., Cederberg, B., & Rasmont, P. (2008). A simplified subgeneric classification of the bumblebees (genus Bombus). *Apidologie*, *39*(1), 46-74.

Williams, P. H., & Osborne, J. L. (2009). Bumblebee vulnerability and conservation world-wide. *Apidologie*, *40*(3), 367-387.

Winfree, R., Williams, N. M., Dushoff J., & Kremen, C. (2007). Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, 10, 1105–1113.

Bumblebee flower visitation count data-set.

Sub-field	Tr.#	Ly	La	Ma	Fj	Po	Ty	Ki	U	TOTAL
A	1	25	28	8		7			1	69
A	2	1	3						2	6
A	3	1	31	4						36
A	4	1	4						2	7
A	5	3	2	2					1	8
A	∑	31	68	14	0	7	0	0	6	126
B	1	10	13	2					6	31
B	2	1	1	1					2	5
B	3	2	3	1					1	7
B	4									0
B	5	5	7	14		5			5	36
B	∑	18	24	18	0	5	0	0	14	79
C	1	4	2	1		1			1	9
C	2	1	2							3
C	3	3	15	9		1			8	36
C	4	5	10	6		6			6	33
C	5	3	4	1		2			3	13
C	∑	16	33	17	0	10	0	0	18	94
D	1		7			2			2	11
D	2	8	2	7				1	13	31
D	3	4	8							12
D	4	2	2	1		1			6	12
D	5	4	12	4		2			4	26
D	∑	18	31	12	0	5	0	1	25	92
E	1	1	1						1	3
E	2	2							1	3
E	3	3	3						2	8
E	4	3							1	4
E	5	2	3	5					4	14
E	∑	11	7	5	0	0	0	0	9	32
F	1			2					2	4
F	2	1	12	1	1				2	17
F	3	1	10	2			1		4	18
F	4	1	8	4					4	17
F	5		1						3	4
F	∑	3	31	9	1	0	1	0	15	60
G	1		2	1	1	1				5
G	2	3	14		1				1	19
G	3	6	16	1		1				24
G	4									0
G	5	4	9	2					2	17
G		13	41	4	2	2	0	0	3	65

Field	Tr.	Ly	La	Ma	Fj	Po	Ty	Ki	U	Σ
H	1	1	5	1					2	9
H	2	2	2	2	1			1		8
H	3									0
H	4	1	3						2	6
H	5	1	2	1						4
H	Σ	5	12	4	1	0	0	1	4	27
I	1	4	3	1					4	12
I	2	1	5	2					3	11
I	3	2	2	1			1			6
I	4	1	6	1	1					9
I	5	7	10	14	1				4	36
I	Σ	15	26	19	2	0	1	0	11	74
Field	Tr.	Ly	La	Ma	Fj	Po	Ty	Ki	U	
	Σ	130	273	102	6	29	2	2	105	649

Ly=Lynghumle = B. jonellus
La=Lapphumle gruppe = B. lapponicus group
Ma=Markhumle = B. pratorum
Fj=Fjellhumle = B. balteatus
Po=Polarhumle = B. polaris
Ty=Tyvhumle = B. wurflenii
Ki=Kilejordhumle gruppe = B. lucorum group
U=Ukjent humle = unknown bumblebee