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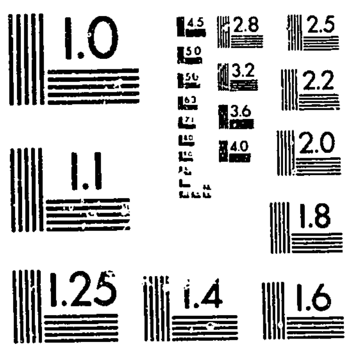

UNIVERSITY OF ALBERTA

PROTECTION FROM HERBIVORY THROUGH ASSOCIATION: THE EFFECT OF RATIO AND SPATIAL PATTERN.

BY

ELENA DIONIS KLEIN ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

The effect of changing ratio and spatial arrangement on the amount and intensity of grazing was examined for two plant species. *Achillea millefolium* var *nigrescens* E. May. (yarrow) is preferred over *Mertensia paniculata* (Ait.) G. Don (bluebell) by *Spermophilus parryii plesius* (Arctic ground squirrels). Five squirrels were presented with various ratios and dispersion patterns of yarrow and bluebell in feeding trials. Grazing pressure was measured at three levels; the amount of plant material consumed, the number of individuals grazed and the rank order of grazing. Grazing was more intense on yarrow when it was present in proportionally smaller numbers than bluebell. Dispersion patterns and ratio treatments had no effect on the overall proportions and number of bluebell plants grazed. Numbers of plants grazed increased as the number of preferred plants present increased.

Results indicate limited, conditional support to the resource concentration hypothesis and the attractant-decoy hypothesis.

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INTRODUCTION

Krebs (1978) defined ecology as the scientific study of the interactions that determine the distribution and abundance of organisms. Interactions with herbivores can have major negative impacts on plant populations (*e.g.*, Fuls, 1992; McAuliffe, 1986; Noy-Meir *et al.*, 1989) necessitating a wide variety of defense responses. As sessile organisms, plants have long been considered to be limited to either mechanical or chemical defenses. Despite much research into plant defenses against herbivores (*e.g.*, Palo and Robbins, 1991; Rosenthal and Berenbaum, 1992; Bernays, 1989; Spencer, 1988), the ecological and evolutionary processes that maintain the effectiveness of chemical defenses are not yet well understood (Marquis 1992). For example, the Red Queen Hypothesis (Van Valen, 1973) predicts that each deterrent produced by a plant will eventually be overcome through evolution by one or more herbivore species and, in turn, a new defense will have to be evolved by the plant. Two problems are immediately apparent when applying this hypothesis to plant-herbivore interactions. The first is that the generation time in plants is often very long compared to the animals that eat them. An oak may live hundreds of years and a herb may reproduce vegetatively for many years. Over that time such plants are exposed to many generations of herbivores that have had a greater opportunity for genetic change that could result in the ability to overcome a plant's defenses.

Secondly, rarely are these defenses completely effective. Herbivores often continue to eat plants that contain substances that are toxic to the grazer (*e.g.*, Meyer and Karasov, 1989). In addition, tolerances are often developed (Brattsten, 1992), and many chemicals only reduce digestibility and therefore only decrease the amount of herbivory rather than prevent grazing completely (*e.g.*, silica, tannins and lignins, Coley *et al.*, 1985). If herbivores can eat these defended plants then how else do plants protect themselves, given the restrictions of long generation times and sessile habit?

Tahvanainen and Root (1972) considered plant communities to contain an "associational resistance" to herbivores that acts beyond the individual plant's or single species' resistance. Root (1973) later referred to this concept as the "the enemies" hypothesis, stating that diverse communities harbor more organisms that compete with, prey upon or otherwise limit herbivore populations than simpler communities. The enemies hypothesis is quite broad and vague since it considered herbivore populations to be controlled by all aspects of the natural biotic and abiotic environment.

Atsatt and O'Dowd (1976) narrowed the focus on associational resistance to the plant community only. They referred to such community resistance as a "plant defense guild" stating that members of such a guild are functionally interdependent as antiherbivore resources. Atsatt and O'Dowd argued that these plant defense guilds increase the length of time that a chemical or morphological defense is effective. When a herbivore has no alternative food source it must physiologically overcome a plant's resistance or perish. Variability in food sources does not encourage specialization, therefore, herbivores that are susceptible to one plant species' defenses can be maintained in communities in which there is a diversity of plant defenses.

Individual plants in communities that provide a diversity of deterrents, which allow herbivores to tolerate small amounts of each toxin, are less likely to suffer complete defoliation than those plants that are found in communities that provide no alternative deterrents. In communities with no alternatives, specialization will be selected for and those individuals that have defenses that are overcome will bear a great deal of grazing pressure. These communities can be viewed as assemblages of palatable, less palatable and nonpalatable food sources and

> '... the probability of a plant being fed upon depends not only on its inherent quality and quantity, but on the chemistry, morphology, distribution, and abundance of alternative prey and nonprey as well'
> (Atsatt and O'Dowd, 1976).

Recent attention to the "plant defense guild" hypothesis has seen the development of the "associational plant refuge" hypothesis (Pfister and Hay, 1988) originally introduced as the "associational plant defence" hypothesis (Hay, 1986). Pfister and Hay (1988) stated that:

> 'An associational plant refuge occurs when a plant that is susceptible to herbivory gains protection from herbivory when it is associated with another plant'.

Research has shown that plants can be protected from herbivory through association and that this protection can occur through differences in a herbivore's food preference. For example, smaller proportions of birch are consumed by voles when associated with alder. Birch is more palatable to voles than alder (Hjalten *et al.*, 1993; see also Gauthier and Bedard, 1991; Atsatt and O'Dowd, 1976; McNaughton, 1978; Parker, 1982).

There are two important hypotheses regarding the mechanisms by which association protects plants from herbivory. First is the "resource concentration" hypothesis (Root, 1973) which states that herbivore abundances will be lower in diverse communities than in simpler communities because herbivores are less likely to locate food sources and will remain in diverse communities for shorter periods. Root developed this hypothesis while working with specialist herbivores but researchers have found it useful in generalist herbivore-plant relations, for example McNaughton (1978) and Gauthier and Bedard (1991). Their research showed that areas that provide a large proportion of less preferred plants (relatively low resource areas) are visited by herbivores less often and for shorter periods.

Second is the "attractant-decoy" hypothesis (Atsatt and O'Dowd, 1976) in which one plant species may be preferentially eaten by a herbivore which will then consume less of neighbouring plant species. If more palatable plants are considered higher resources then this hypothesis overlaps with Root's resource concentration hypothesis. These two hypotheses approach the same problem from two different scales. The resource concentration hypothesis views associational protection at the level of the stand. The attractant-decoy hypothesis explains associational protection at the level of the individual plant. Neither mechanism can work if herbivores are not selecting some plant species preferentially over others.

There is evidence supporting each of the hypothesized mechanisms, but the universality and effectiveness of each mechanism is unclear for several reasons. First, how a herbivore divides its foraging within plant communities while maintaining at least a minimal intake of nutrients is complex (*e.g.*, Belovsky and Schmitz, 1991; Pennings *et al.*, 1993; Illius *et al.*, 1992; Danell *et al.*, 1991). Grazers have been shown to be affected by social learning (*e.g.*, Peacock and Jenkins, 1988), a need for a mixed diet, (*e.g.*, Pennings *et al.*, 1993; Westoby, 1978), density of plants (*e.g.*, Bach, 1989; Kareiva, 1982; Lundberg and Danell, 1990), and size as well as composition of a stand of plants, (*e.g.*, Hjalten *et al.*, 1993; Andersen, 1990; Illius *et al.*, 1992; Bach, 1986).

Second, in associations which confer protection to one plant species, the benefit to that plant is clear but the cost to plants close to it are not. For example, when one plant species suffers less herbivory due to association, does the plant species it is close to experience greater defoliation?

Third, grazers do not always have the luxury of choice of foraging areas; once a herbivore is in a stand of plants will it consume the same amount of food in an area containing large proportions of preferred foods as in areas where the majority of plants are less preferred, but still palatable?

Fourth, plants often have the ability to recover from partial predation and they can be made up of free living, genetically identical ramets of different ages. These features make it difficult to assess the biological significance of the damage sustained by a grazed plant.

Finally, scale is a problem when determining plant species associations from both the plant's and the herbivore's view point. At what scale plant associations are determined depends upon quadrat size. At what scale a herbivore views proximity will depend on the animal's size, morphology, digestive capacity and grazing time constraints (Laca and Demment, 1991).

Researchers have also had difficulty with the evolutionary importance of associational defenses. It is difficult to determine how effective this type of defense can be to sessile organisms with limited influence over where they grow and what their neighbour is. The significance that clonal growth has to associational defense has been overlooked (but see Thomas 1990).

Clonal plants have the ability to either produce patches that contain high ratios of themselves through "phalanx" growth patterns, or to spread out and mix with other members of the plant community through "guerilla" growth (Bell 1984). If a herbivore responds to plant associations at the same scale as a patch of clones grows then growth patterns may be important to defense.

This study investigates two aspects of plant associations. Firstly, by examining the effect that specific ratios have on how a generalist herbivore (*Spermophilus parryii plesius*) divides its foraging on preferred and less preferred plant species (*Achillea millefolium* var *nigrescens* and *Mertensia paniculata* respectively), the mechanistic hypotheses of associational protection are evaluated.

Assuming that stands of preferred plants are high resource areas, the resource concentration hypothesis predicts less foraging when ratios of preferred to less preferred plants are low than when ratios are high. This hypothesis has always been examined when foragers are free to roam from stand to stand. By keeping ground squirrels in one type of stand while manipulating ratios, the effect that the ratio of preferred to less preferred plants has on grazing pressure can be isolated from herbivore movement. I predict that ground squirrels will eat less plants in the low resource stands despite spending equal amounts of time in these stands as in high resource stands.

The attractant-decoy hypothesis predicts that foraging will be directed towards the preferred plants. I would then expect less grazing pressure on less preferred plants when in association with large amounts of preferred plants than when less preferred plants are in monoculture.

The second aspect of association that this study investigates is the effect of spatial patterns that mix preferred plants with less preferred or separates them. This is a test of the scale in which the trials are presented. If association is important at a scale smaller than the feeding trials then a difference will be apparent when the same proportions of plant material are presented in different spatial arrangements. I predict that spatial patterns that separate preferred plant species from less preferred result in greater grazing on the preferred than patterns that mixed plant species. This will provide information that can be used to assess the significance of clonal growth on associational protection.

In order to estimate treatment effects this study measures grazing at three levels, the number of individuals attacked, the proportion of plant material consumed and the rank order of attack. By assessing grazing pressures at several levels the relative importance of associational protection to the individual, clone and population can be addressed.

In this paper the term "plant" or "individual" refers to a cutting within a single peat pot. Individuals that are known to be genetically identical are "ramets" and a population of ramets is a "clone".

METHODS

STRUCTURES

Holding and feeding trial cages

Ground squirrels were housed in outdoor cages at the Kluane research base of the Arctic Institute of North America (61N 138W). Each holding cage was 1.0 X 1.0 X 0.5 m, contained a 0.6 X 0.25 X 0.25 m high wooden- or tin-covered hiding area, ample straw, mouse cotton, a water bottle and food. Cages for female ground squirrels also contained a cardboard (nest) box (.2 X .2 X .1 m) containing mouse cotton. The cage was protected from rain by plywood and from heat by burlap bag shading. The walls, floor and ceiling were made of one inch hardware cloth. Each cage sat on plywood to facilitate walking for the squirrels and cleaning. Each holding cage was connected to a feeding trial cage by a 100 mm rigid plastic tube with an aluminum sliding trap door. The trap door was operated by a string and pulley system that could be controlled from a central blind.

Each feeding trial cage was 1.23 X 1.23 X .43 m high. Each was made with one inch hardware cloth, a plywood floor and a wooden frame. The roof hinged open to allow access for measuring and planting of the herbs. Seven cm of sand covered each floor. No shade or rain protection was provided for feeding trial cages. Squirrels were allowed free access to feeding trial cages whenever the cages were not needed for planting.

COLLECTION AND CARE OF STUDY ORGANISMS

Arctic ground squirrels

Arctic ground squirrels (*Spermophilus parryii plesius*) were captured over a period of nine days in mid May 1993 using Tomahawk live traps (Tomahawk Live Trap co., Tomahawk, Wisconsin, U.S.A., 16.5 X 16.5 X 48.0 cm). Squirrels were trapped along the old Alaska highway in locations central to the plant collections. Captured ground squirrels were weighed and their sex determined. Three males and two pregnant females were retained.

Each squirrel was given an unique combination of dye marks using Clairol "Nice and Easy" natural blue-black hair dye (Clairol Canada, unit of Bristol-Myers Squibb Canada Inc.). When not undergoing feeding trials, squirrels were fed rabbit chow *ad libitum* (Shur-gain rabbit ration pellets) as well as one sixth of a medium sized apple per day. Pregnant and lactating females were given double and triple apple rations, respectively. Once a week, during cage cleaning, squirrels were trapped with a peanut butter baited Tomahawk trap placed in the feeding trial cage and weighed (Figure 1).

The two females gave birth on May 23 and June 1, after 5 and 14 days in captivity respectively. Their young emerged from the nest boxes within the holding cages 25 to 27 days later. After emergence their holding cages were outfitted with a 75 mm polyvinyl chloride tube which allowed the juveniles freedom to travel between the surrounding boreal forest and the holding cage. Nine days after emergence the juveniles were trapped and released where their mother was originally captured. For these nine days no feeding trials were conducted for the females as the juveniles could follow them into feeding trials and because females may have been distracted. All remaining squirrels were released when natural populations began to hibernate (August 8, Tim Karels, pers comm. University of Toronto).

Plants

Achillea millefolium var *nigrescens* (yarrow) and *Mertensia paniculata* (bluebell) were collected from roadsides from kilometer 1670 to kilometer 1700 of the Alaska highway. Plant collecting began in late May, approximately two weeks after snow melt in the area. Previous research had indicated that yarrow may be grazed in greater quantities than bluebell by Arctic ground squirrels (Hubbs, 1993). As many as 120 individuals were collected per site and care was taken to never collect more than one third of a population in any one site. Sites were situated a minimum of one kilometer apart. Plants were collected with a minimum of one leaf and a maximum of three. A portion of rhizome no longer than 1 cm was included. A total of 4500 individuals of each species were collected.

In a shaded nursery the plants were dipped in indol-3-butyric acid (0.4%) rooting powder (Stim-root No 2, Plant Products Co. Ltd. Bramalea, Ontario) and planted in expanded number seven jiffy pellets (Jiffy Co. Ltd., Norway). After expansion in water the jiffy pellets were soaked in a mixture of 300 ml of 5% 10-52-10 fertilizer (Plant-prod Plant Starter Fertilizer, Plant Products Co. Ltd.) and 200 ml of 1% Nodamp fungicide (Oxine benzoate, Plant Products Co. Ltd.). Plants were misted with water and left in propagation trays covered with clear plastic. Plants were watered as necessary but not fertilized again.

After four weeks the plants were ready to use in feeding trials. Plants that showed signs of root formation, had a minimum of two and a maximum of four leaves and no flower buds were used.

TRIAL PROCEDURES

Plantings

Each feeding trial consisted of one of three different spatial arrangements of plants and one of five different ratios of the two plant species. The three spatial arrangements were: i) rows - 54 plants arranged in seven staggered rows, each plant separated by 4.5cm, (Figure 2a), ii) mixed patches - 54 plants arranged in nine circular patches, separated by 15 cm, with six plants per patch, two species per patch (Figure 2b), and iii) unmixed patches - 48 plants arranged in eight circular patches (Figure 2c). Between one and five ratios of yarrow to bluebell plants were presented in each spatial arrangement (Table 1). One trial of each of the nine treatment combinations is considered a series.

Squirrels were allowed free access to feeding trial cages for six days before feeding trials began. The afternoon before a feeding trial, squirrels were locked out of the feeding trial cages and their view of it obscured by cardboard. During this time yarrow and bluebell were planted into the sand such that the pots were not visible. Each feeding trial was presented to each squirrel once and then the whole series of nine trials was repeated until the squirrels were released at the end of the summer. The nine feeding trials could be presented in six unique series such that no trial followed another more than once in all series, this would avoid autocorrelation. All of these six unique series were used in the trials and each squirrel was randomly assigned to one or more different series.

Feeding trials took place from late June to early August. Data from the first few trials on each squirrel were not used. Initially females consumed everything in a 20 minute period whereas males ate considerably less, sometimes as few as seven of the fifty-four plants. For this reason trial times were set at 10 minutes for females and 20 minutes for males.

The night before a feeding trial, food was removed from each squirrel's holding cage between 9:30 and 10:00 p.m.. The morning of a feeding trial the number of leaves and the lengths of the lamina (leaf blade) were recorded for each planted herb. Two squirrels that were awake and moving within their cages were selected to undergo trials. Observers sat in a blind facing the feeding trials cages, the trap doors between the feeding trial cages and the holding cages were lifted and the trials began once the squirrel first entered the feeding trial cage. Observers recorded the order the available plants were selected by the squirrel, the time spent in and out of the feeding trial cage and the order in which the plants were grazed. After the squirrel had been in the feeding trial cage for the designated time, they were chased back into their holding cages and the trap door closed.

All herbs were examined for signs of grazing and length measurements were made on damaged leaves on the day of the trial. The view between the holding cages and the feeding trial cages were again blocked during measurements. All herbs were removed and new ones were planted for the next trial. The number of days available between snow melt and hibernation of the squirrels was not sufficient to allow each squirrel to undergo only one trial per day and still provide replication for each trial. Therefore, each squirrel occasionally underwent two trials on the same day.

Squirrels that had not come out for a trial or were not going to be tried before one p.m. were given their apple ration by mid morning. Pregnant or nursing females were also given one tablespoon of rabbit chow. After the last trial for an individual squirrel it was given rabbit chow *ad libitum*. Water was always available to the squirrels and they were often observed to drink even during feeding trials.

ADDITIONAL DATA COLLECTION

Associations on active burrow sites

In order to determine at what scale yarrow and bluebell are associated in nature, contiguous quadrats (quadrats placed end to end) were used at ten active ground squirrel burrow sites. Surveys were done in late July and early August before bluebell leaves began to turn red. All the burrow sites used were situated on mounds of soil and contained more than five entrances. The first quadrat was set at one end of the mound and the last at the end furthest to that. Since each burrow site was a different size, the number of 0.2 x 0.2 m quadrats used per site varied. Activity of burrow sites was assessed by placing tiles coated with talcum powder at each burrow entrance late at night and then examined for signs of ground squirrel activity early the next morning (Boonstra *et al.*, 1992 and references therein). These survey sites were chosen because ground squirrels were observed feeding at them.

ANALYSIS

The effects of the three spatial patterns, the five different ratios of yarrow to bluebell and variation between the squirrels on the amount that each plant species were grazed was investigated. Variables of interest were: the total number of plants grazed, the percent of available yarrow or bluebell grazed, the proportion of each species' leaf length that made up the diet of the squirrels, the proportion of each species' leaf length that was removed, and the order in which ground squirrels chose plants.

All proportional data were transformed to the arcsine of the square root for analysis (Zar, 1984). Multiple comparison procedures were done by hand; other analyses were done using SAS for Windows version 6.03 and SYSTAT version 5.03.

When no significant difference was found between spatial pattern treatments, trials with the same ratio were combined to increase sample size on subsequent analyses. The exception is the unmixed patches which were never combined with the other 3:3 ratios.

Effect of treatment on number of plants grazed

The sum of yarrow and bluebell plants that were grazed at least partially were used in a general linear model (glm) ANOVA. Not all squirrels were involved in all treatments therefore, the experimental design is a mix of factorial and nested ANOVAs (see table 1). Therefore, the three spatial patterns were analyzed using separate ANOVAs with ratio and squirrel as levels within them. The effect of spatial pattern was tested by calculating the sum of squares for each of the three tables, adding the error terms and calculating an overall F statistic. This was not standard procedure so a second method was also employed.

The dependance of being grazed on spatial pattern was tested with a contingency table. This method could not distinguish the effect of ratio from spatial pattern until the table was subdivided for each ratio of yarrow.

Significantly unequal means were subsequently investigated with a Tukey test for unequal sample sizes

(Zar, 1984). Means for Tukey tests and for figures were produced by including all squirrels used in the trials even when variation amongst them were high. This decision was based on the premise that plant communities are likely to experience herbivory from many different individuals and so the mean effects are of interest.

The number of plants grazed in the first three patches visited was determined for the 3:3 mixed and unmixed patch trials. Only plants grazed during the first visit to each of these three patches were counted. For some plants it was not possible to determine whether it had been grazed during the first or second visit. In these situations the plant was included in the tally for mixed patches but not for unmixed patches. This made the t-test of the two means conservative.

Percent of yarrow or bluebell grazed

The number of each species that are ungrazed may be important to the fitness of a clone or population. If grazing is sufficiently intense or a plant species is particularly susceptible to herbivory then those individuals that are not grazed at all may be the only ones contributing to further reproduction. In order to compare the different ratios in a meaningful way, the percent of the available individuals that were grazed at least partially was calculated for each species. Data were transformed to proportions. The effect of spatial pattern was then tested with a 2 x 3 contingency table. The effect of ratio and squirrel were investigated with a glm ANOVA.

Numbers of individuals of each species were not compared across ratios because the number available varied for each ratio.

Proportion of leaf length removed for each species

The above analyses only considered the numbers of plants grazed. In order to investigate the intensity of grazing the length of leaf blade removed was analyzed.

$$L_i = x_i / y_i$$

Where:

L_i = the proportion of leaf length of species *i* removed in a trial.

x_i = the total leaf length removed in a trial of all individuals of species *i* (one value per feeding trial)

y_i = the sum of leaf lengths of all individuals of species *i* available before the feeding trial. Treatment effects were examined with a glm ANOVA.

Pearson's correlations were employed on the total leaf length of plants prior to a trial and the proportion of leaf length that was eaten (Zar, 1984).

Logistic regressions were used to determine whether the total length of leaves on a plant could predict whether it would be grazed (Hosmer and Lemeshow, 1989).

Proportion of each species in diet

Preference for yarrow or bluebell was investigated by examining the proportions of the diet that were yarrow or bluebell. Although squirrels had access to other foods, comparisons between the relative proportion of yarrow and bluebell consumed are referred to as proportions in the diet. This terminology separates this analysis from other, similar, comparisons explained above and approximates usage in preference literature.

$$P_i = x_i / z$$

Where:

P_i = proportion of species *i* in diet

x_i = the total leaf length removed in a trial of all individuals of species *i* (one value per feeding trial)

z = the total leaf length removed in a trial for all individuals (both species summed, one value per feeding trial).

The effect of spatial pattern on P_i was tested with a t-test.

Jacobs' mortality quotient (a modification of the foraging index; Jacobs, 1974) was employed to compare changes in diet composition while accounting for the varying total consumption of each squirrel, the differing total density of plants in some trials and the changing ratios of the two plant species. This index was chosen because of the predictability of relationships of variables used in the model and because of its biological relevance (see appendix). This method is robust to changes in relative density of plant species being compared.

The effect of varying ratios and preference on Jacobs' mortality quotient is presented in the appendix.

$$Q = P_i(1-n_i) / n_i(1-P_i)$$

$$J = \log (Q)$$

where:

J = Jacobs' mortality quotient

P_i = proportion of species *i* found in the diet

n_i = proportion of species *i* found in the trial

The value of J is large and positive when $P_i>n_i$, and correspondingly large and negative when $P_i<n_i$.

Rank choice

The number of yarrow and the number of bluebell that were amongst the first nine plants grazed was determined for all mixed species trials. These data were translated to proportions of the nine plants, arcsine-square root transformed and then employed in a t-test (Zar, 1984). Proportions of yarrow to bluebell were then compared to trial ratios.

The average rank for yarrow and for bluebell was determined for each ratio and each spatial pattern.

Associations on active burrows

Numbers of yarrow and bluebell present in each quadrat were analyzed using a three term covariance method (Dale and Blundon, 1991). Scale of pattern is adjusted from the quadrat size at which analysis suggests pattern by the correction term suggested by Dale and Blundon.

RESULTS

The various ratios used as treatments in this study held when numbers of individuals of yarrow and bluebell were compared, that is a 5:1 ratio contained 45 yarrow plants and 9 bluebell plants. However, the total length of leaves of a bluebell plant ranged from 26 to 106 mm while yarrow ranged from 37 to 281 mm. This discrepancy in the range of total leaf length of the two species as well as leaf length differences between individuals of the same species resulted in ratios of leaf length different from that intended. However, five distinct treatment groups still existed (Figure 3). Leaf length is a good predictor of the likelihood of being grazed (logistic regression $G=31.958$,$p<0.001$ for bluebell and $G=72.184$,$p<0.001$ for yarrow). The largest leaves of both species being most likely to be grazed.

NUMBER OF PLANTS GRAZED

Total number of plants grazed

The total number of plants grazed (yarrow + bluebell) was affected mostly by ratio but also by squirrel behaviour (Tables 2 and 3). Spatial pattern had no significant effect.

The total number of plants (yarrow + bluebell) that were grazed decreased when the ratio of yarrow to bluebell was low. Monocultures of the yarrow were grazed most heavily and trials containing proportionally more bluebell than yarrow were grazed least (Figure 4).

Mixed patches of the 3:3 ratio had a mean of 8.7 (s.d. 4.43) plants grazed before a squirrel moved to a fourth patch, whereas squirrels in unmixed 3:3 trials visited a mean of 11.1 (s.d. 4.01) plants. That difference is not significant ($t=-1.312$, $p=0.204$).

Number of each species grazed

The percent of bluebell plants and the percent of yarrow plants that were grazed by squirrels were unaffected by spatial pattern (yarrow $G=1.449$, $p=0.484$; bluebell $G=3.272$, $p=0.195$).

Variation amongst squirrels had an effect on the percentage of bluebell grazed, whereas ratio provided the greatest amount of variation in the percentage of grazed yarrow plants (Table 4).

The highest percent of grazed yarrow plants occurred in 1:5 ratios in which there were only nine yarrow plants (Figure 5), but this was not different from the percent of yarrow plants grazed in monoculture, or from the unmixed patch trials.

Yarrow is disproportionally represented in the number of plants grazed indicating a preference for yarrow (Figure 6). The contribution that yarrow makes to the number of grazed plants decreases as the number of yarrow available decreases.

AMOUNT OF PLANT MATERIAL REMOVED

There is a small but significant correlation between the proportion of leaf material removed and the total leaf length when planted for both species (yarrow: $r>0.095$, $p<0.001$; bluebell: $r=0.081$, $p<0.001$).

Proportion of each species' leaf length removed

Spatial pattern had no effect on the proportion of leaf material removed. The proportion of leaf length removed in a trial was significantly affected by squirrel for both species and by ratio for yarrow alone (Table 5).

Yarrow underwent heaviest grazing when it was present in low ratios (Figure 7, t=7.279, p<0.001). Moreover, the individuals within these low ratios were grazed very heavily with an average of over 50% losing 75% or more of their leaf length. Contrast this to 19% of yarrow plants grazed over 75% in trials containing large proportions of yarrow plants. Bluebell plants were rarely grazed heavily (Table 6, Figure 8).

Proportions of plant species in diet

In most mixed species trials (52/60 trials, p<0.001, Figure 9) yarrow made up a greater proportion of the diet of Arctic ground squirrels than the proportion that was present in the feeding trial. Bluebell was usually grazed proportionally less (59/60 trials, Figure 10). These results indicate a preference for yarrow and an avoidance of bluebell.

Figures 11 and 12 present the results of Jacobs' mortality quotient. There was a large spread of values among trials, and no trend was apparent.

Rank choice

Of the first nine plants that squirrels grazed in two species feeding trials, 82% were yarrow (Figure 13). Over half of the first nine plants grazed in 1:5 trials were yarrow, although only nine yarrow plants were present. The proportion of yarrow in the first nine grazed plants is significantly greater in 5:1 trials than in 1:5 trials (t=-4.011, p<0.001).

The proportions of yarrow and bluebell grazed within the first nine plants was not related to the ratio of yarrow and bluebell in the trial (Figure 13).

The average rank of the first nine plants grazed was near five for yarrow in all mixed species trials and in five of the seven trials for bluebell (Table 7).

Associations on active burrows

At eight of ten burrow sites bluebell and yarrow showed consistent negative association at a scale of about 140 cm (i.e. 6-8 quadrats, Table 8).

DISCUSSION

It is both a virtue and a difficulty of plants that the loss of fitness of a single ramet can bear little importance to the overall fitness of its clone. In the course of a decade a clone may be grazed frequently, each season new ramets surviving or succumbing to the appetites of various herbivores. The lifetime impacts of this herbivory are a much more meaningful measure of the importance of damage than the effects of a single grazing event. Furthermore, the same percentage of tissue loss on two plants is not always comparable; the age of the leaves lost can affect the seriousness of damage to plants (Sand-Jensen and Jacobsen, 1994) as can the timing of the loss (Doak, 1992). Despite these difficulties, some important characteristics of the damage done to yarrow and bluebell in this experiment can further the understanding of how important association is as a form of protection.

Dirzo (1984) succinctly summarizes the important events in herbivore-plant encounters as: a) the probability of encounter, b) the likelihood of herbivory upon encounter and c) the consequences of herbivory. The resource concentration hypothesis predicts less time spent feeding in low resource areas which would translate to a lower probability of encounter for individual plants. In this study, trials with low numbers of yarrow and high numbers of bluebell could be considered low resource trials. As predicted, ground squirrels spent less time grazing in trials with low resource concentrations. That is, the total number of plants grazed in these trials was less than in trials with high resources. It would not be surprising to find that when ground squirrels have a choice, they would leave such low resource patches quickly.

The stepwise results of the total number of plants grazed to the number of yarrow present also suggests that the ratio of preferred to less preferred could have an important effect on how long a herbivore stays in any foraging area. However, bluebell was not grazed more in low resource trials whether this is measured by the percent of plants grazed or the proportion of leaf material removed. There were more bluebell plants in low than in high resource concentration trials so the actual number of plants grazed was higher (i.e. 25% of 45 plants is more than 25% of 9 plants). As the total number of plants grazed indicates, there was sufficient time for squirrels to graze more bluebell had they so chosen. If these 45 plants had been spread out into five high resource concentration areas and a herbivore visited each area then just as much damage to bluebell would be expected.

Yarrow was disproportionately represented among the first nine plants grazed. If squirrels are moving constantly then the attractant properties of yarrow may protect bluebell more than was observed. These results also suggest that the relative differences between the preferred and less preferred plants species are important in determining how effective the attractant-decoy hypothesis is to any situation. If two plant species are preferred very differently it could be expected that a herbivore would travel some distance to graze the preferred plants while passing over the less preferred. However, if the two species are similar in preference then a herbivore may not increase foraging time to find the more preferred and instead graze the less preferred as it comes across it. McNaughton's (1978) research indicated that a preferred plant is protected from wildebeest and buffalo by association with less palatable species. However, the more selective Thomson's gazelle and zebra were not affected by the presence of less preferred plants. Unfortunately, McNaughton did not present data on the amount consumed of the less palatable plants.

The attractant-decoy hypothesis predicts that should a herbivore be in a site the probability of attack would be less for bluebell when yarrow is available. As this hypothesis predicts, yarrow did bear the brunt of grazing pressure by ground squirrels in both number of plants grazed and amount of plant material removed. However, there was no significant difference between trials with yarrow and damage done in bluebell monocultures and the relative numbers of yarrow had no appreciable effect on bluebell. Grazing of bluebell was significantly affected by the individuality of the squirrels alone. In some trials bluebell was not grazed at all when yarrow was present. This never occurred in bluebell monocultures but its importance is unclear especially when bluebell was often grazed while some yarrow remains. This suggests that at times a bluebell individual may have more appeal than a yarrow individual.

Neither mechanistic hypothesis specifically addresses the consequences of herbivory. As stated above, there are many factors that contribute to the severity of any grazing event. It is safe to generalize that the greater the amount of plant material removed, the greater the likelihood that fitness will be reduced. To that end, yarrow did best in trials in which it was present in larger numbers, because the smallest proportion of leaf material per plant was removed.

Without information on how the probability of a squirrel visiting a site is affected by ratio, it is difficult to determine whether association between yarrow and bluebell should be expected in nature. However, from this study we can predict that if encounter is likely, then yarrow in higher numbers is better off than those in low numbers. For bluebell the benefits of such an association is less clear cut, but small numbers of individuals may result in those few being ignored.

Active ground squirrel burrows are areas in which the probability of encounter is high. Surveys on such sites indicated that the two species are negatively associated at a scale smaller than an arena. Many factors may influence the association of two plant species, and this study is not extensive enough to determine whether associational protection is important in determining where yarrow and bluebell grow. However, if negative association at such a scale is under the influence of herbivory then this should have been apparent in the unmixed patch trials. Results from these trials were remarkably similar between all spatial arrangements. The exceptions to this are in the percentage of yarrow plants grazed in mixed and unmixed trials. It is tempting to speculate that the concentration of yarrow plants resulted in easier access for ground squirrels (cf 3:3 unmixed to monocultures). The conservativeness in determining the mean number of plants visited per patch before leaving for a fourth patch makes this assumption even more inviting. However, the inclusion of the unmixed patch trial in the multiple comparison procedure in Figure 5 may have increased the type one error rate because spatial arrangement was shown to have no significant effect in the glm ANOVA (Day and Quinn, 1989). So this result must be viewed with some caution.

Nevertheless, this is an interesting avenue for future research and present speculation. Plants have limited "choice" in their neighbours; because of this the evolutionary importance of associational protection has not been clear. Is this protection merely a coincidental event that allows some species to exist in areas where herbivory would otherwise exclude them or is it a defense mechanism exploited by plants and selected for? It has been shown that neighbours can exert some influence on the growth patterns of plants (Turkington and Klein, 1993). Clonal organisms that exhibit phalanx type growth can create patches that are high concentrations of themselves. Guerilla growth patterns result in ramets being spread further and spaced amongst neighbours. A plant that is high on the ranking of preferred species in an area may do better if it is present in high proportions. Phalanx growth patterns through short rhizomes or stolons and many branches would result in higher densities of that species' ramets. Grazing pressure may be an indication of how apparent the plant is to the local herbivores and may have some impact on the growth responses of ramets.

The amount of variation in individual squirrel feeding behaviour could affect the ratios of preferred to less preferred plants that provide effective protection in any specific plant community. Given that herbivores die, lose their territory and that different species of herbivores may overlap territories, any control over growth patterns associated with protection from herbivory would be most effective if they were flexible. Phenotypic responses would then be a better strategy than genotypic responses, allowing environmental tracking (Turkington *et al.*, 1994).

The different total amounts of plant material present in the ratios is a confounding factor. Producing the 9000 cuttings necessary for these experiments at an uniform size was unfeasible. As stated, leaf length of yarrow seemed to have some effect on the proportion consumed but the effect on the probability that it was grazed varied. Squirrels were observed to eat the longest, oldest leaves first on any plant they were grazing. These leaves made up the majority of the total leaf length and this may have been the reason for the correlation.

There was limited evidence that bluebell benefited from associational protection in these experiments. High resource and low resource trials resulted in similar results for bluebell. Occasionally bluebell was ignored in mixed species stands which provides some evidence for the attractant-decoy hypothesis. For yarrow the results disagree with the resource concentration hypothesis. Proportions of yarrow consumed in these trials suggest that high resource stands may provide more protection than low resource stands assuming that herbivores do not visit the former more often than the latter. These results viewed from the attractant-decoy hypothesis could be expected. As the attractant, yarrow populations may avoid depletion by providing more plant material than the herbivore cares to consume.

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APPENDIX

JACOBS' MORTALITY QUOTIENT

$$Q = P_i(1-n_i) / n_i(1-P_i)$$

$$J = \log(Q)$$

where Q = Jacobs' mortality quotient

P_i = proportion of species *i* found in the diet

n_i = proportion of species *i* found in the trial

Since J is dependent upon both the proportion presented in a trial and the proportion grazed it is a measure of the decrement of yarrow and bluebell in a feeding trial. These values have a predictive relationship (Figure 14) and are not sensitive to changes in abundance, as is the foraging ratio, so they allow quantitative comparisons when ratios vary between trials (Jacobs 1974).

The measurement of decrement of the two plant species is useful when considering the effect of selective feeding on a plant community, however, as only two plant species were used in these feeding trials the values of J for each are dependent (J for yarrow = -J for bluebell).

Table 1. The nine treatments used in feeding trials with Arctic ground squirrels. Ratios are yarrow to bluebell. See Figure 2.

Spatial pattern	Ratio	number of plants in trial
Rows	0:6	54
	1:5	54
	3:3	54
	5:1	54
	6:0	54
Mixed Patches	1:5	54
	3:3	54
	5:1	54
Unmixed Patches	3:3	48

Table 2. Total number of plants grazed (yarrow + bluebell) in feeding trials with Arctic ground squirrels. Trials were one of three different spatial patterns. See Figure 4.

Source	Sum of Squares	df	Mean Square	F-ratio	p
Unmixed patch trials					
Squirrels	241.233	3	80.411	3.181	0.106
Error	151.667	6	25.278		
Mixed patch trials					
Ratio	516.570	2	258.285	4.451	0.300
Squirrels	624.264	3	208.088	3.586	0.039
Ratio X Squirrel	36.848	6	6.141	0.106	0.994
Error	870.500	15	58.033		
Row trials					
Ratio	2254.636	4	563.659	4.617	0.005
Squirrels	349.845	3	116.615	0.955	0.426
Error	3906.405	32	122.075		
All trials					
Spatial pattern	414.708	2	207.345	2.230	>0.20
Error	4928.572	53	92.992		

Table 3. Goodness of fit to the Chi squared distribution for the effect of spatial arrangement on the number of yarrow plants grazed in feeding trials with Arctic ground squirrels.

Ratio	**G-statistic**	**df**	**p**
1:5	not calculated		
3:3	0.000	1	1.00
5:1	2.456	1	0.117

Table 4. Effect of ratio and squirrel on the percent of available a) yarrow and b) bluebell grazed by Arctic ground squirrels. See Figure 5.

a) yarrow

Source	**Sum of Squares**	**df**	**Mean Square**	**F-ratio**	**p**
Ratio	1.711	3	0.570	12.29	0.0001
Squirrel	0.214	3	0.071	1.53	0.2160
Ratio X Squirrel	0.440	8	0.055	1.18	0.3254
Error	2.506	54	0.046		

b) bluebell

Ratio	0.595	3	0.198	2.32	0.0857
Squirrel	2.132	3	0.711	8.30	0.0001
Ratio X Squirrel	0.583	9	0.065	0.76	0.6559
Error	4.711	55	0.086		

Table 5. Effect of treatment on the proportion of available leaf material removed from a) yarrow and b) bluebell by Arctic ground squirrels. See Figures 7 and 8.

a) yarrow

Source	Sum of Squares	df	Mean Square	F-ratio	p
Unmixed patches					
Squirrel	0.151	4	0.038	1.661	0.275
Error	0.136	6	0.023		
Mixed patches					
Ratio	0.845	2	0.422	23.329	0.000
Squirrel	0.356	4	0.089	4.914	0.010
Ratio X Squirrel	0.197	8	0.025	1.360	0.289
Error	0.272	15	0.018		
Rows					
Ratio	0.723	3	0.241	5.82	0.0032
Squirrel	0.116	4	0.029	0.70	0.5991
Error	1.160	28	0.041		
All trials					
Spatial pattern	0.194	2	0.097	3.031	>0.5
Error	1.568	49	0.032		

b) bluebell

Source	Sum of Squares	df	Mean Square	F-ratio	p
Unmixed patches					
Squirrel	0.308	4	0.077	1.609	0.287
Error	0.287	6	0.048		
Mixed patches					
Ratio	0.075	2	0.037	1.897	0.184
Squirrel	0.787	4	0.197	9.993	0.000
Ratio X Squirrel	0.130	8	0.016	0.824	0.595
Error	0.295	15	0.020		
Rows					
Ratio	0.106	3	0.035	0.300	0.825
Squirrel	0.683	4	0.171	1.455	0.255
Ratio X Squirrel	0.376	12	0.031	0.267	0.988
Error	2.229	19	0.117		
All trials					
Spatial pattern	0.296	2	0.148	2.114	>0.5
Error	2.811	40	0.070		

Table 6. Yarrow and bluebell plants with more than 75% of leaf length removed by Arctic ground squirrels. Numbers are percentages and standard deviations of the total number of individuals of that species present at the beginning of a feeding trial. Values are averages of feeding trials with a total density of 54 plants.

Ratio	yarrow (%)	bluebell (%)	n
0:6	-	7 +/- 3.4	9
1:5	63 +/- 21.2	6 7.4	18
3:3	33 25.5	11 5.5	21
5:1	19 13.8	8 16.3	21
6:0	29 20.1	-	

Table 7. Average rank and standard deviation of a) yarrow and b) bluebell within the first nine plants grazed in mixed species feeding trials. See Figure 13.

a) yarrow

Ratio:	Mixed Patches		Rows		Unmixed Patches
1:5	4.7	+/- 2.71	4.9	+/- 2.45	-
3:3	5.0	2.62	5.0	2.54	4.8 +/- 2.58
5:1	4.9	2.60	4.7	2.51	-

b) bluebell

Ratio:	Mixed Patches		Rows		Unmixed Patches
1:5	5.2	+/- 2.45	4.6	+/- 3.01	-
3:3	4.9	2.71	4.2	2.54	5.0 +/- 2.83
5:1	5.0	*	6.3	3.06	-

* n=1, no standard deviation

Table 8. Association of yarrow and bluebell at nine active Arctic ground squirrel burrow sites. Negative associations indicate that the two species tend not to be found together at approximately the reported scale on that burrow site. The units of scale are number of 0.2 x 0.2 m quadrats.

Scale	**association**
6	negative
7	positive
7	negative
7	negative
8	negative
9	negative
7	negative
6	negative
6	negative

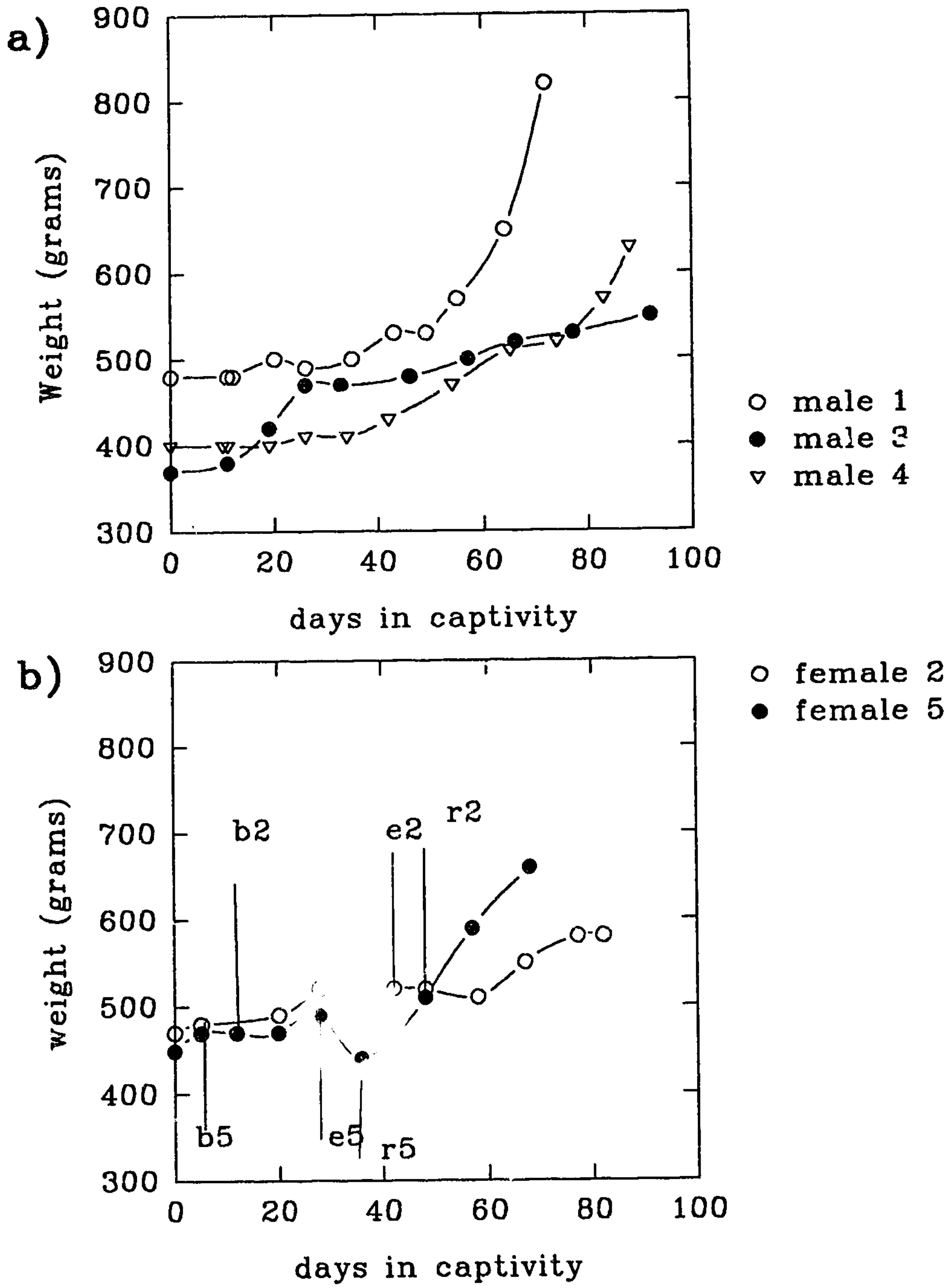
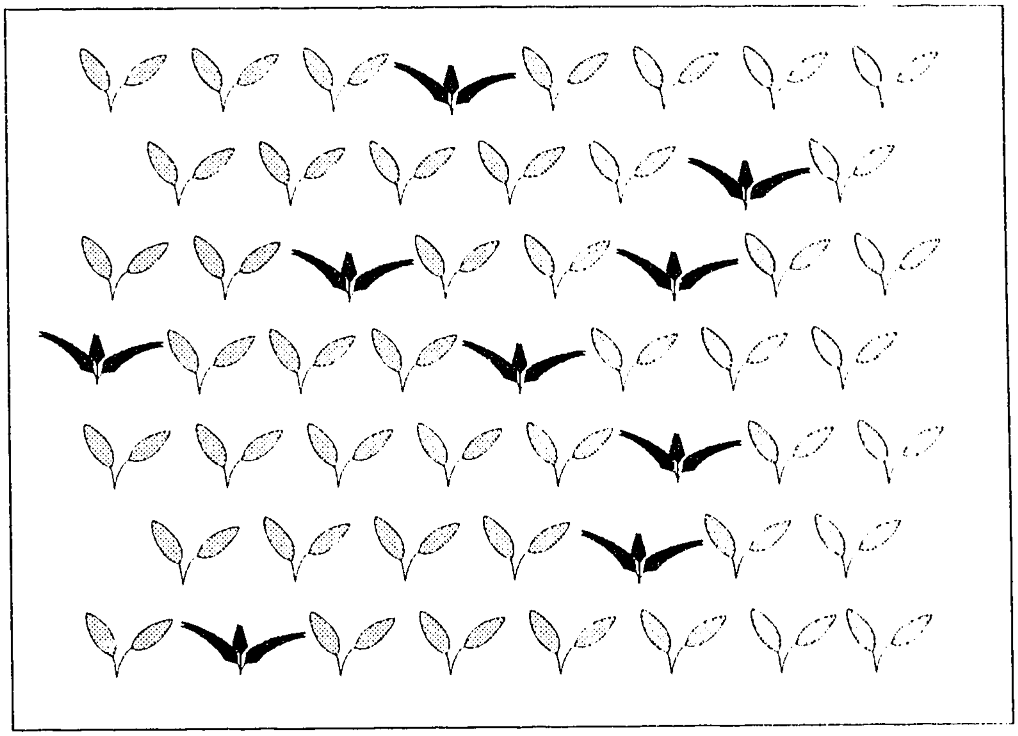
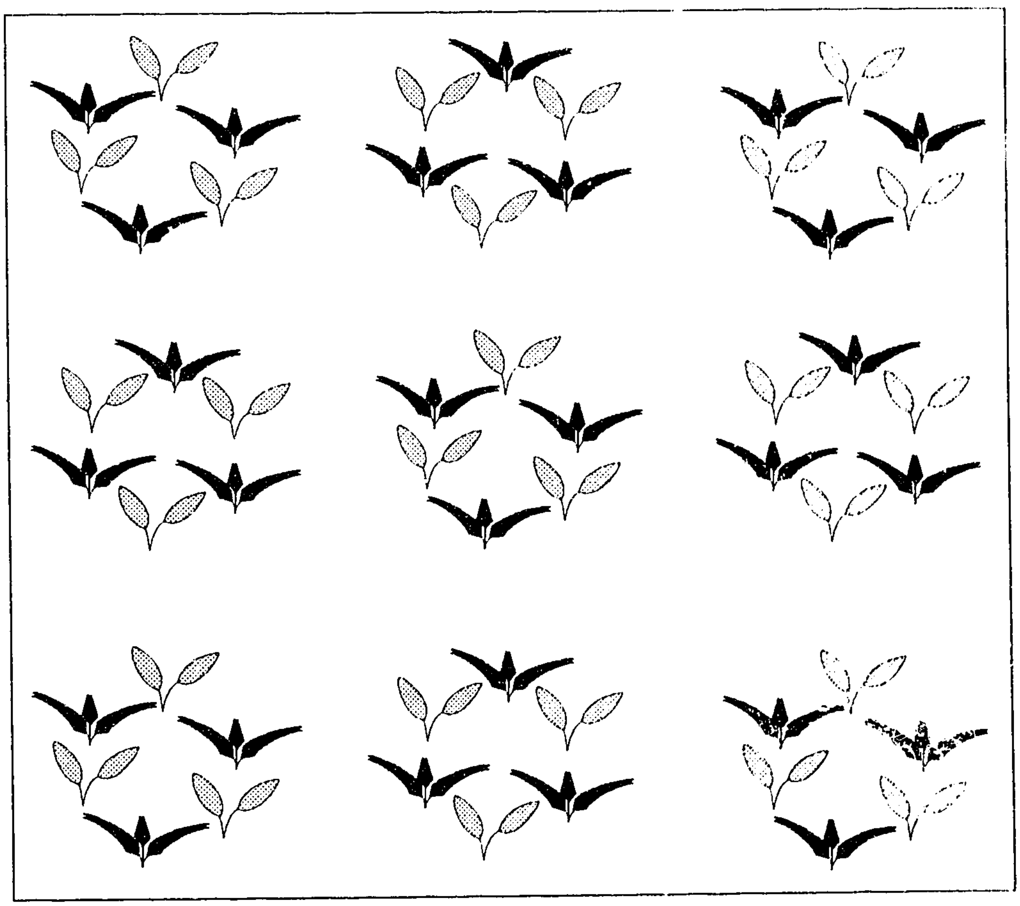


Figure 1. Weight of the a) three male and b) two female squirrels during captivity. Dates that squirrels gave birth (b), juveniles emerged (e), and juveniles were released from captivity (r) are marked for each female (2, 5). Day 0 for each squirrel ranged from May 13 to 18.

a)



b)



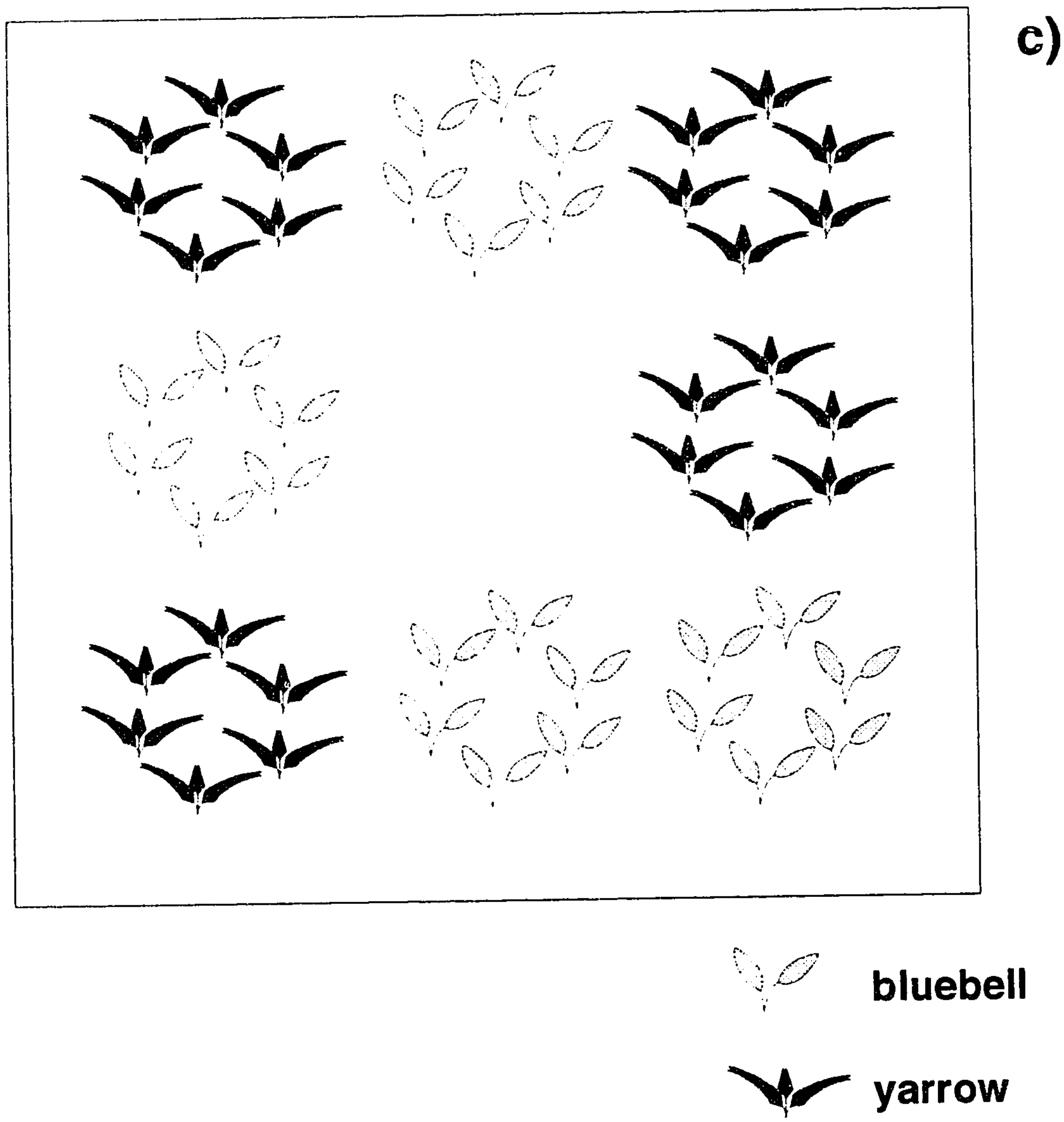


Figure 2. The three spatial arrangements used in feeding trials with Arctic ground squirrels. a) Rows—54 plants in seven staggered rows. b) Mixed patches—54 plants in nine circular patches, each containing a total of six individuals of yarrow and bluebell. c) Unmixed patches—48 plants in eight circular patches, each containing a total of six individuals of one species. Refer to text for further explanation.

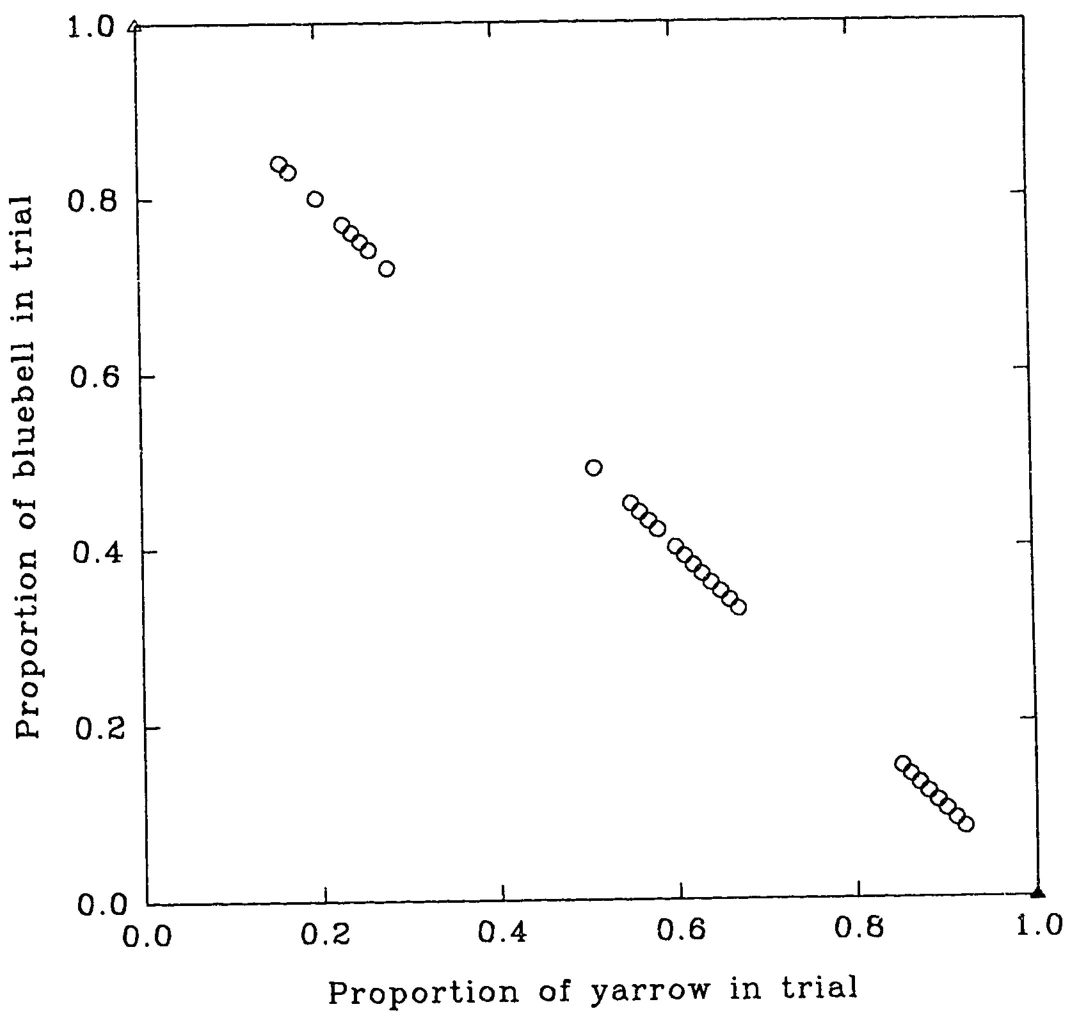


Figure 3. The five distinct treatment groups of varying proportions of yarrow and bluebell as determined by leaf length (see Figures 7–12). Treatments were used in feeding trials with Arctic ground squirrels. Hollow triangles represent eight trials, solid triangles represent nine trials and circles are one trial each.

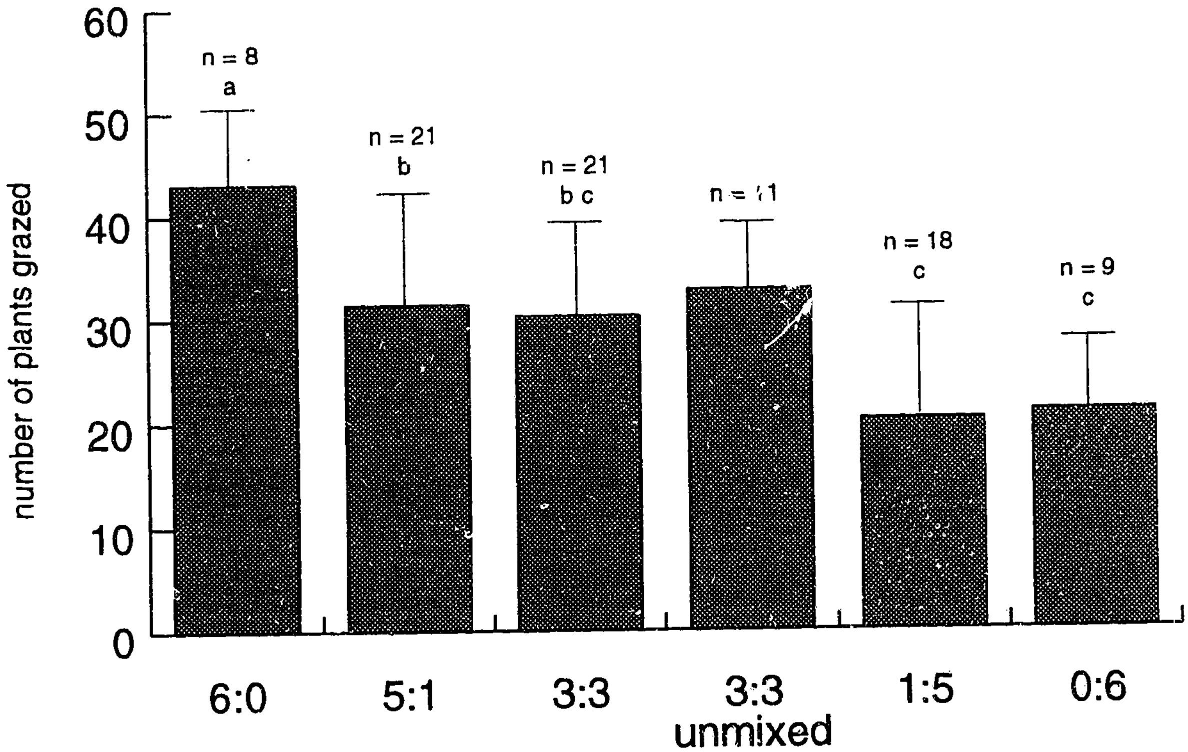
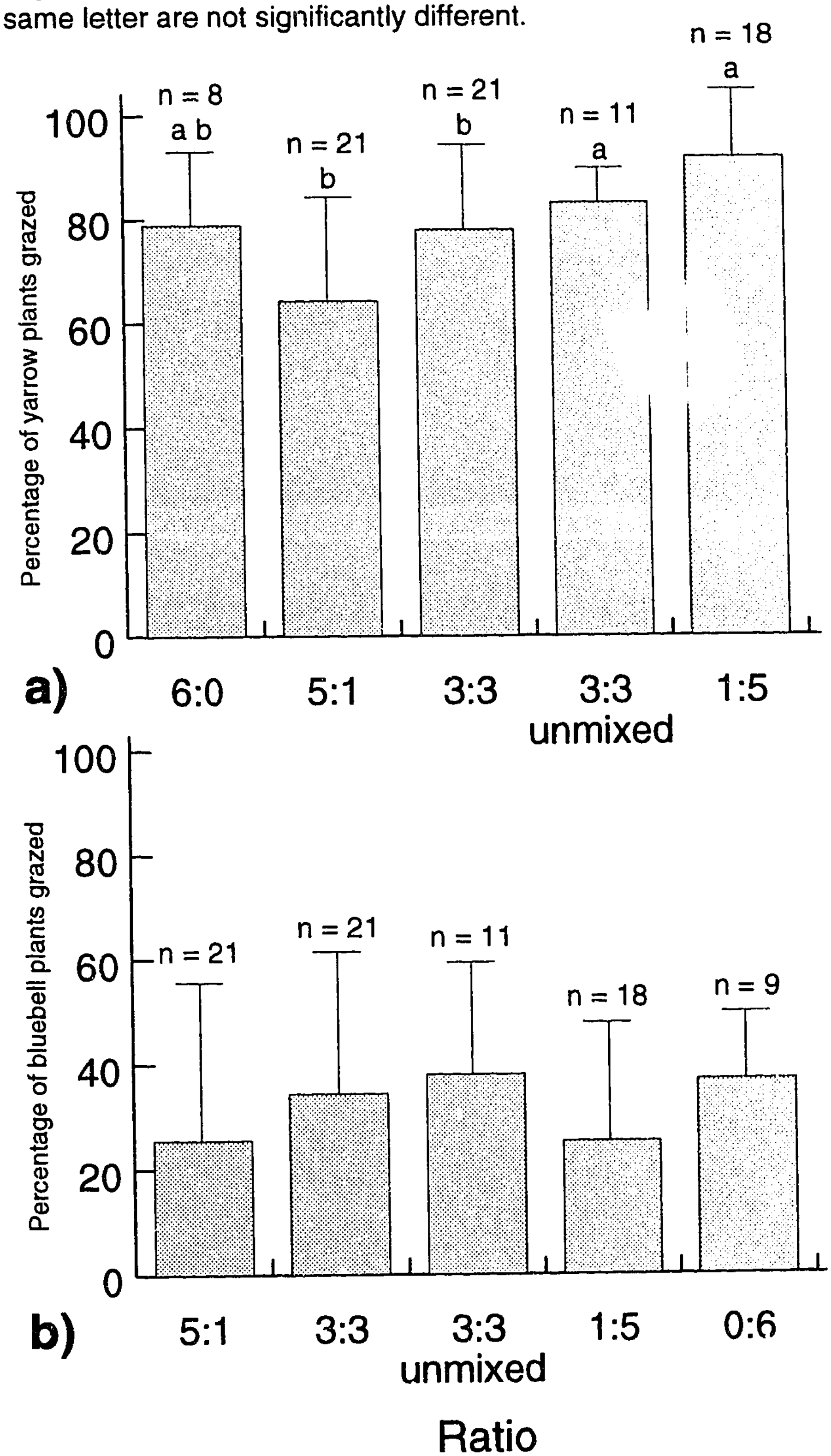


Figure 4. Total number of plants (yarrow + bluebell) grazed by Arctic ground squirrels in feeding trials. Error bars represent standard deviations, ratios are yarrow to bluebell, and n refers to number of trials. Bars with the same letter are not significantly different from each other. The 3:3 unmixed patch trials contained 48 plants; all others had 54. The 3:3 unmixed patch trials were not included in the multiple comparison procedure.

Figure 5. Percentage of a) yarrow and b) bluebell individuals grazed by Arctic ground squirrels in feeding trials. Each trial contained 54 plants of varying ratios of yarrow to bluebell. Error bars represent standard deviations. Bars with the same letter are not significantly different.



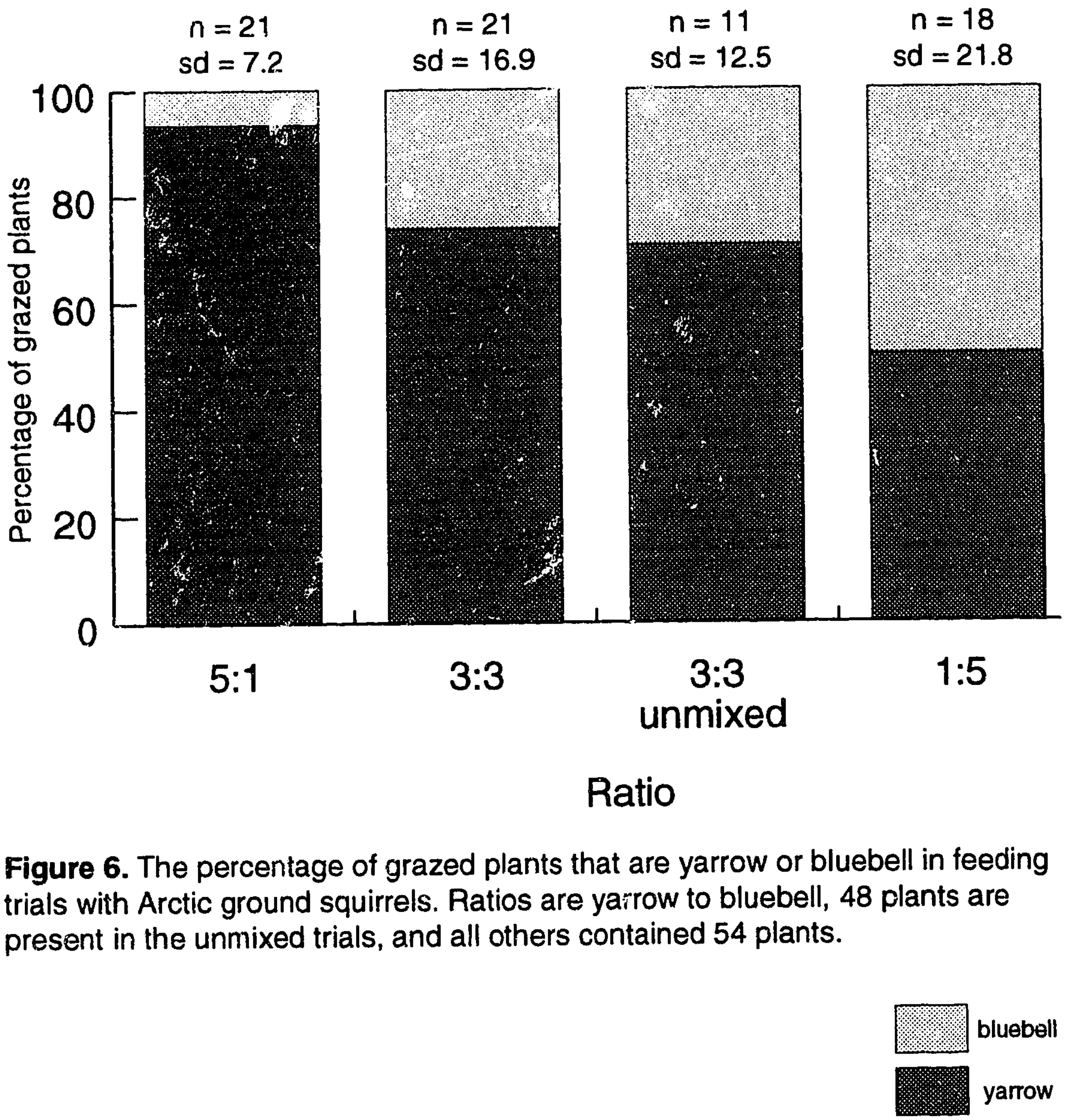


Figure 6. The percentage of grazed plants that are yarrow or bluebell in feeding trials with Arctic ground squirrels. Ratios are yarrow to bluebell, 48 plants are present in the unmixed trials, and all others contained 54 plants.

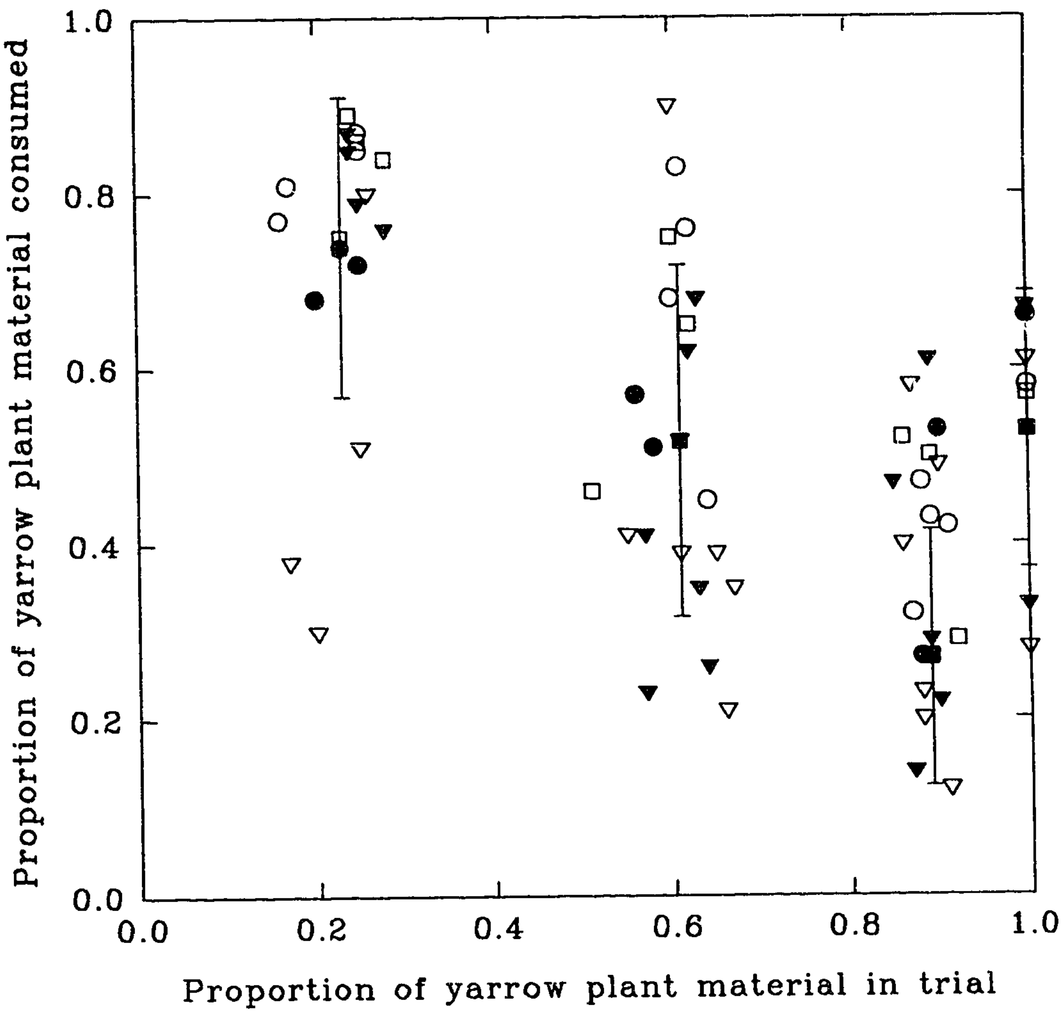


Figure 7. The proportion of available yarrow that is consumed by Arctic ground squirrels when the proportion present varies. Each point represents a single feeding trial with a total density of 54 plants of two species.

○ squirrel 1
● squirrel 2
▽ squirrel 3
▼ squirrel 4
□ squirrel 5
■ mean and sd

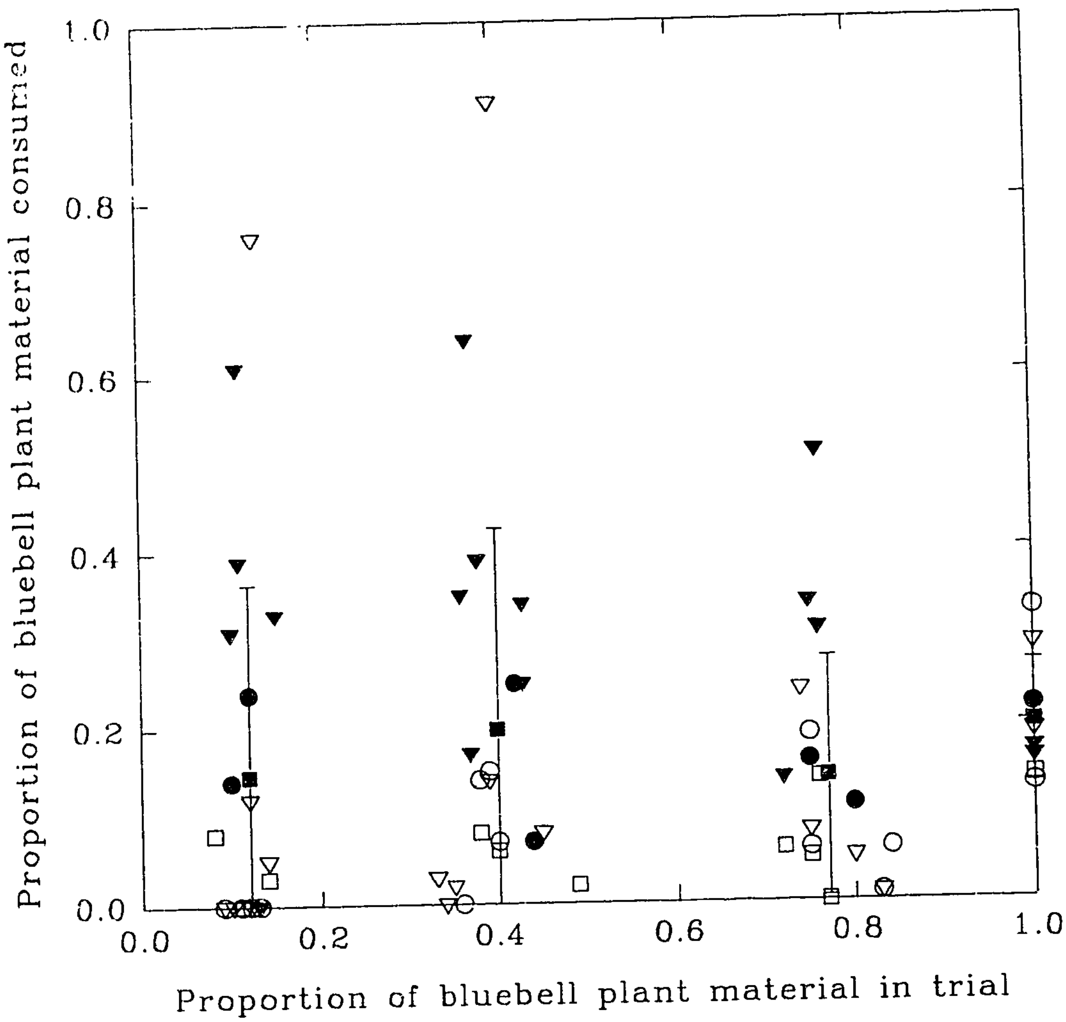
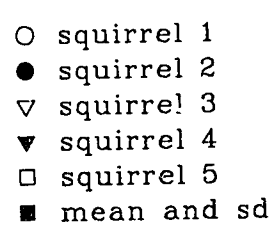


Figure 8. The proportion of available bluebell that is consumed by Arctic ground squirrels when the proportion present varies. Each point represents a single feeding trial with a total density of 54 plants of the two species.



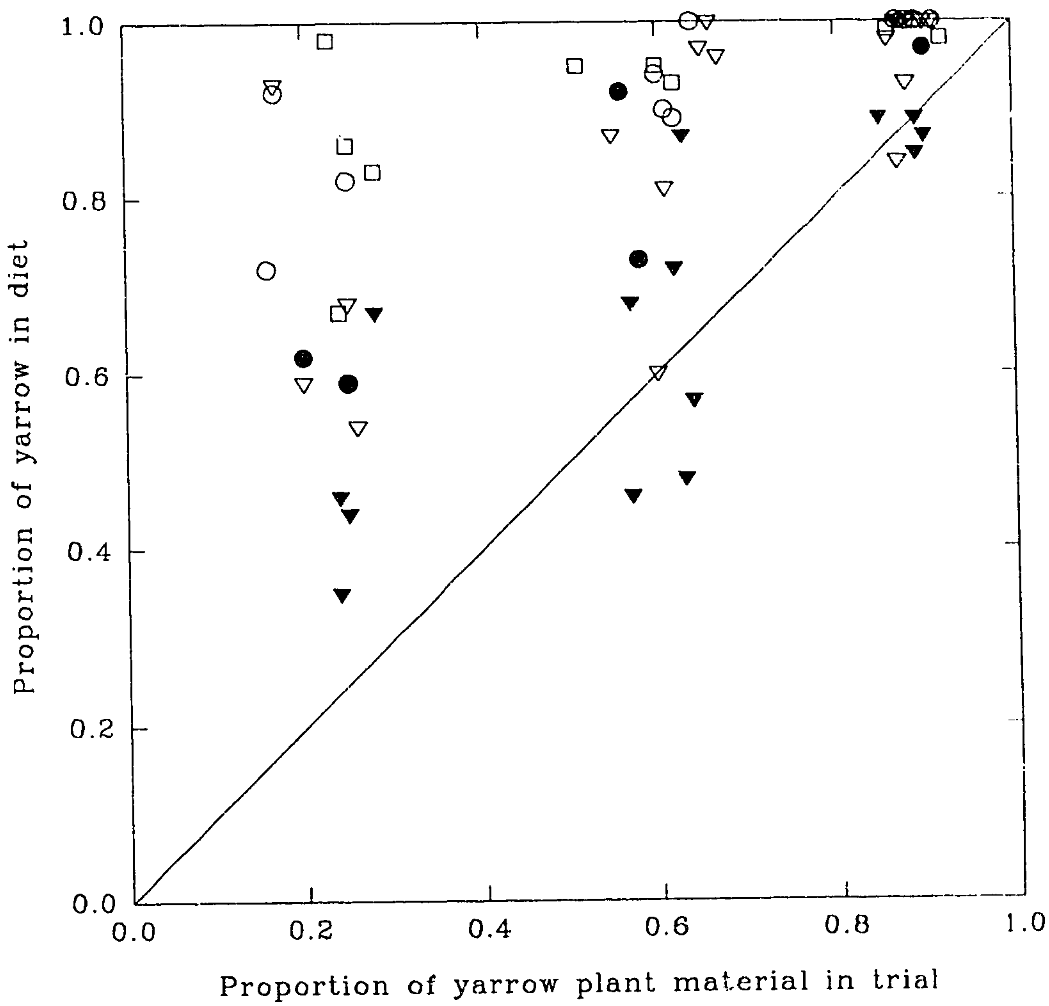


Figure 9. The proportion of yarrow composing the diet of Arctic ground squirrels when the proportion of yarrow available varies. Each point represents one feeding trial with a total density of 54 plants of two species. Values below the line are trials in which squirrels consumed proportionally less yarrow than was available.

○ squirrel 1
● squirrel 2
▽ squirrel 3
▼ squirrel 4
□ squirrel 5

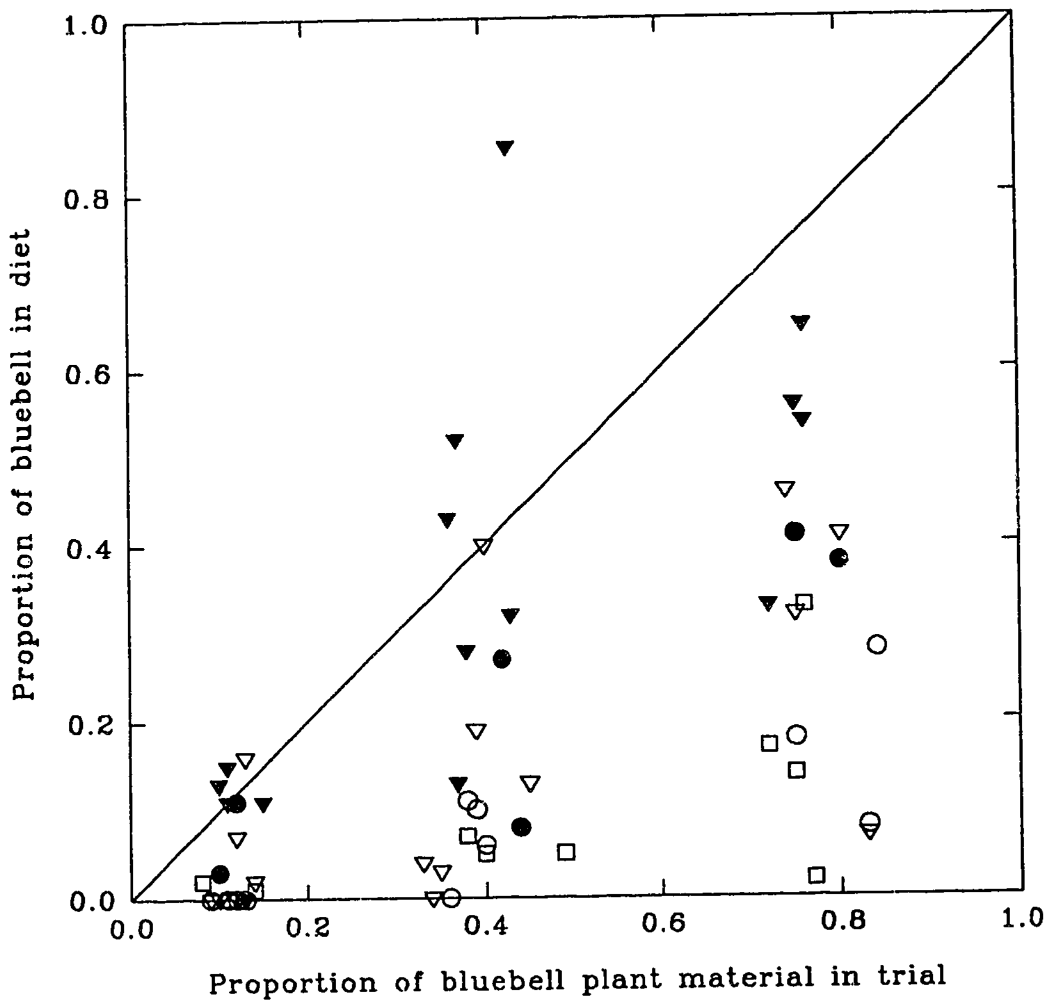


Figure 10. The proportion of bluebell composing the diet of Arctic ground squirrels when the proportion of bluebell available varies. Each point represents one feeding trial with a total density of 54 plants of two species. Values above the line are trials in which squirrels consumed proportionally more bluebell than was available.

○ squirrel 1
● squirrel 2
▽ squirrel 3
▼ squirrel 4
□ squirrel 5

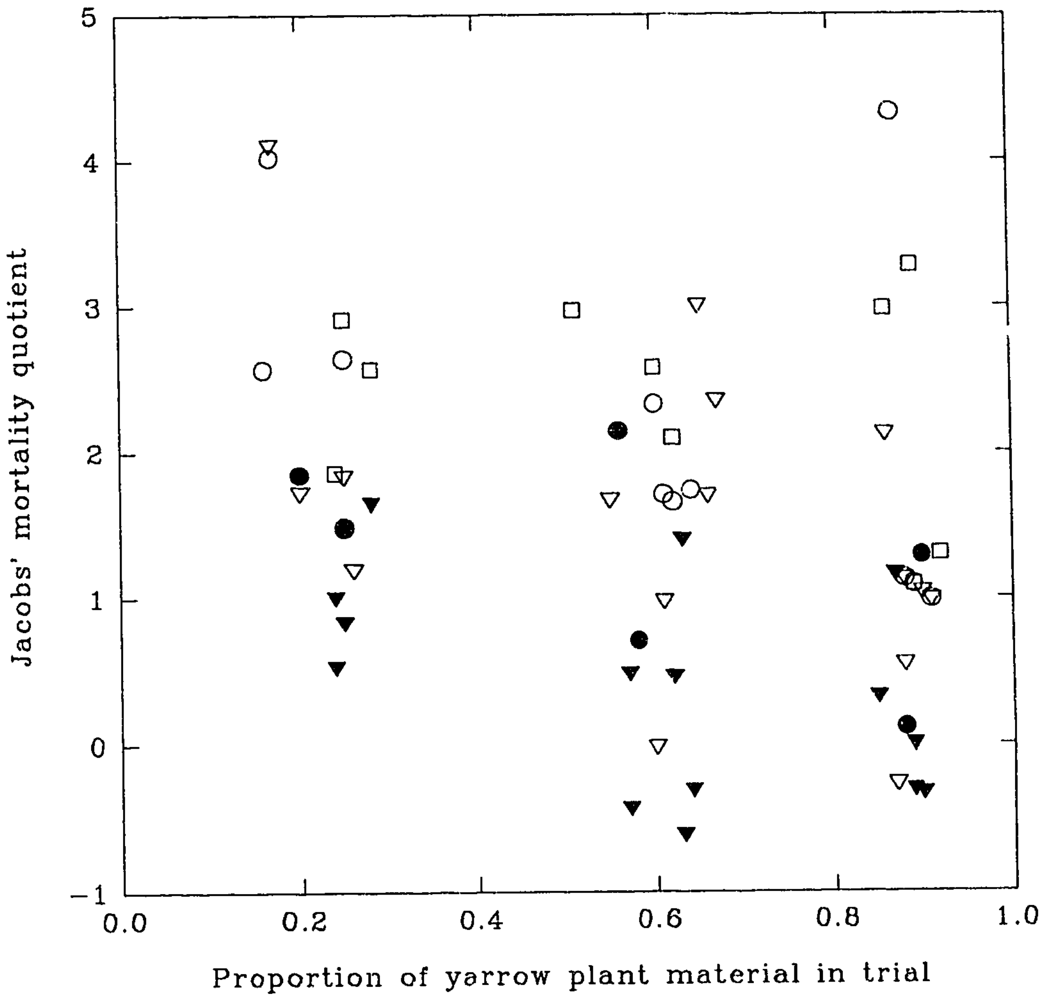
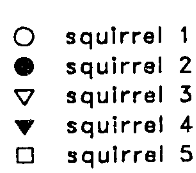


Figure 11. Jacobs' mortality quotient for yarrow when presented in varying proportions of the total density of plants in feeding trials with Arctic ground squirrels. Each point represents a single feeding trial with a density of 54 plants.



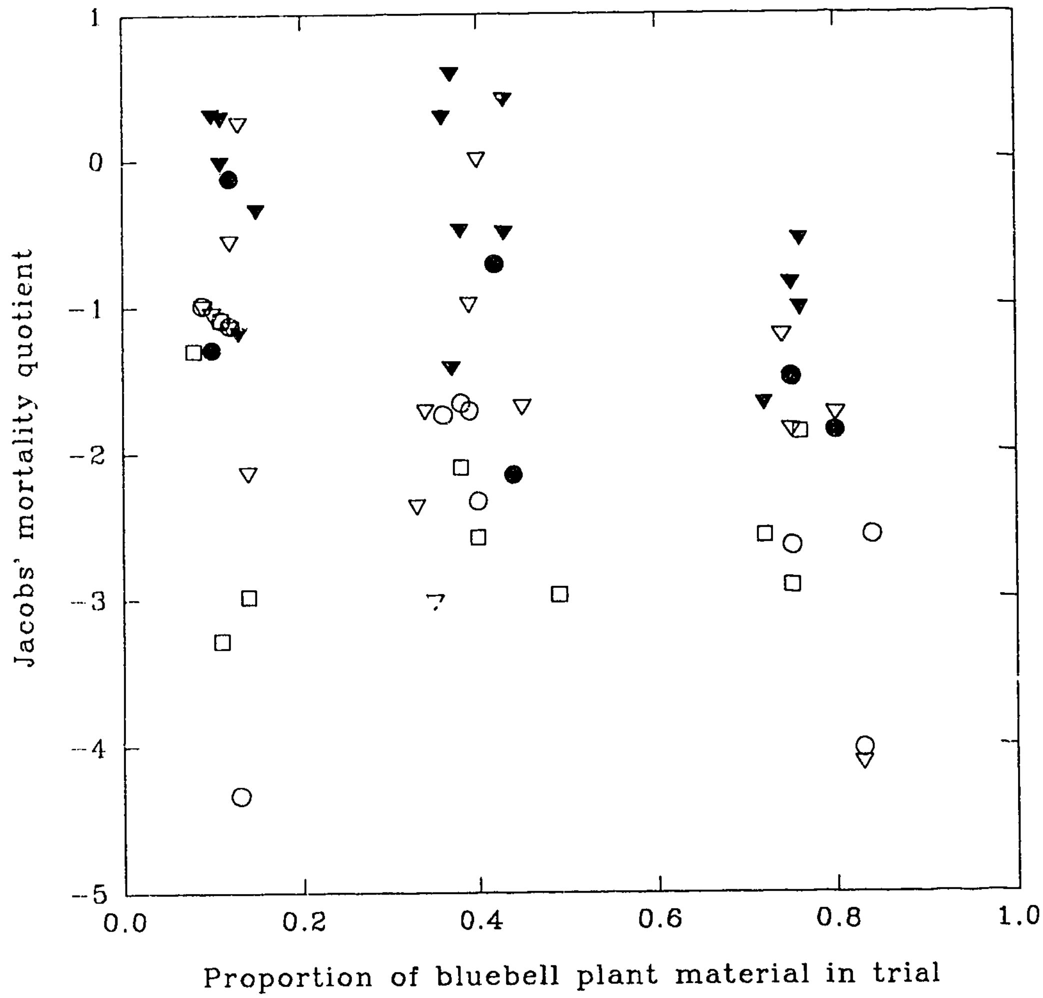


Figure 12. Jacobs' mortality quotient for bluebell when presented in varying proportions of the total density of plants in feeding trials with Arctic ground squirrels. Each point represents a single feeding trial with a density of 54 plants.

○ squirrel 1
● squirrel 2
▽ squirrel 3
▼ squirrel 4
□ squirrel 5

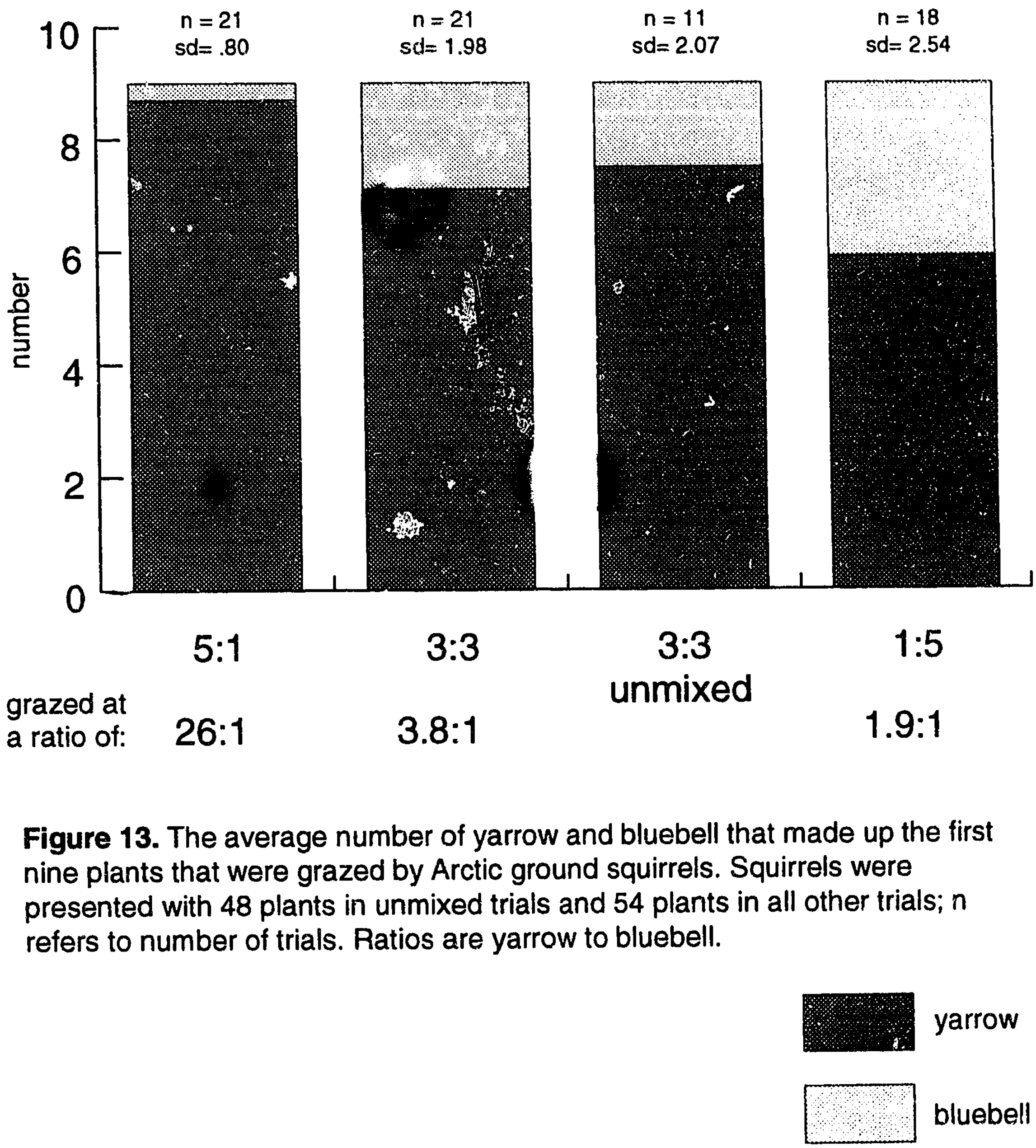


Figure 13. The average number of yarrow and bluebell that made up the first nine plants that were grazed by Arctic ground squirrels. Squirrels were presented with 48 plants in unmixed trials and 54 plants in all other trials; n refers to number of trials. Ratios are yarrow to bluebell.

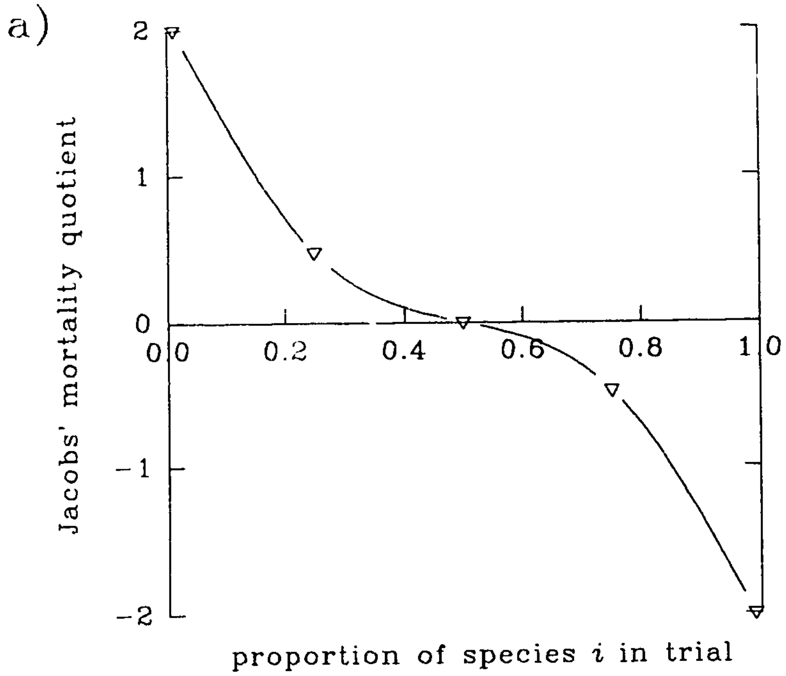


Figure 14. Values for Jacobs' mortality quotient when a) proportion of species i is fixed in diet and varies in trial; and when b) proportion of species i is fixed in trial but varies in diet.