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Master Thesis

合歡山地區冷鐵杉混合林中台灣高山田鼠的覓食生態：探討植物特性的影響

Foraging Ecology of Taiwan Field Vole (*Microtus kikuchii*) in a Taiwan Fir-Taiwan Hemlock Forest at the Hehuan Area: Effects of Plant Attributes

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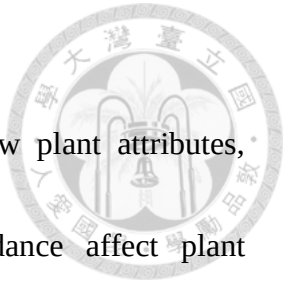
摘要

草食動物的覓食生態學有一重要議題在探討植物特性(如：化學特性、物理特性以及相對豐度)如何影響草食動物的覓食選擇；同時這也協助我們預測草食動物對植物群聚造成的影響。室內的植物可食度實驗和野外的動物食性分析，兩者結合，提供了了解覓食生態的重要資訊。台灣高山田鼠(*Microtus kikuchii*)為台灣特有種。先前研究已研究了高山草原中高山田鼠的覓食生態。本研究旨在了解在合歡山冷鐵杉混合林中植物特性對台灣高山田鼠的覓食生態之影響。我分析三個季節中(三月、七月以及十一月)台灣高山田鼠的食性，並同時進行餵食實驗，後者包含了五種優勢植種：玉山箭竹(*Yushania niitakayamensis*)，玉山鬼督郵(*Anisliaea reflexa*)，裂葉樓梯草(*Elatostema trilobulatum*)，玉山擬鱗毛蕨(*Dryopsis transmorrisonensis*)以及日本曲尾苔(*Dicranum japonicum*)。我分別檢測五種植物的七種化學成分、硬度和相對豐度。結果顯示，高山田鼠的食性主要由玉山箭竹組成，並且不同植種對田鼠有不同的可食度。而在食性結果具有季節上的差異。化學成分對可食度具有顯著的影響：粗蛋白對可食度有正向的影響。另外，硬度對可食度有顯著的負向影響。基本上，食性分析和可食度的結果相吻合。總言之，在高山森林內對高山田鼠來說玉山箭竹仍是最重要的食物來源，植物特性也對可食度具有顯著的影響。

關鍵字：台灣冷杉林、食性分析、可食度、台灣高山田鼠、玉山箭竹



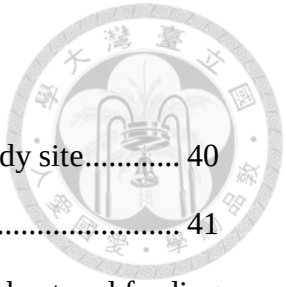
Abstract

A key aspect of herbivore foraging ecology investigates how plant attributes, including chemical, physical characteristics, and relative abundance affect plant palatability and herbivore diets, which, in turn, help us predict the impact of herbivory on plant communities. The Taiwan field vole (*Microtus kikuchii*) is an endemic species in Taiwan. Previous studies have investigated its foraging ecology in alpine meadows. In this study, I aimed to understand the foraging ecology of Taiwan field voles in a Taiwan fir-Taiwan hemlock forest at the Hehuan area. I analyzed the diets of Taiwan field voles and conducted palatability feeding experiments in three seasons (March, July, and November). Five dominant plants were included in feeding experiments: *Yushania niitakayamensis*, *Anisliaea reflexa*, *Elatostema trilobulatum*, *Dryopsis transmorrisonensis* and *Dicranum japonicum*. I measured 7 chemical compounds, toughness, and relative abundance of the 5 species. The results showed that vole diets were mainly composed of *Yushania niitakayamensis*, which was also the most palatable plant. Different species had different palatability to voles. Vole diets showed significant seasonal effects. Chemical characteristic of plants affected palatability: crude protein had a positive effect. Furthermore, toughness had a negative effect on palatability. Besides, the results in diet analyses and palatability experiments were generally

consistent with each other. In conclusion, *Yushania niitakayamensis* remains the most important food resource for Taiwan field voles in alpine forest. Plants attributes significantly influence palatability.

Key words: Taiwan fir forest (*Abies kawakamii)*, diet analysis, palatability, Taiwan field vole (*Microtus kikuchii*), Yushan cane (*Yushania niitakayamensis*)

Content



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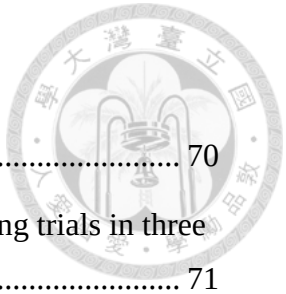


Content of Figures

Introduction

Foraging ecology of herbivores investigates how herbivores interact with plants (Olff & Ritchie, 1998; Provenza *et al*., 2003). Herbivores can change plant communities by selectively consuming plants, which reduce the relative abundance of plants they prefer (Wu & Shih, 2010). Herbivores often choose from the variety of plants based on plants' quality, i.e., biochemical and physical attributes. The consumed plants affect herbivores' body growth rates, reproduction, and population density (Cole & Batzli, 1979). Plants may, in turn, respond to herbivore consumption by altering biochemical and physical attributes. Therefore, understanding what herbivores prefer to eat in the fields, and why, are important for predicting the effects of herbivory on plant communities and of plants on herbivore populations. It is thus critical for inferring how herbivores and plant communities will be impacted by the changing environment (Litvaitis, 2000).

Herbivore diet and palatability of plant to herbivores are two basic pieces of information needed to predict the effect of herbivory (Kimball & Provenza, 2003). Diet analysis gives information on what herbivores eat in the field; palatability gives information on how much a plant would be consumed under a controlled environment. The two pieces of information support each other. Although some studies have found

that results of diet analyses were similar to those of palatability (reviewed in Batzli, 1985), either information alone is not sufficient to predict the impact of herbivory on vegetation for two reasons: (a) preferred food is prone to be eaten first in the nature, certain plant species tend to be underestimated in diet analyses (Batzli & Pitelka, 1983); (b) palatability is not measured in a natural setting, thus could give artificial information (Batzli, 1985).

Both herbivore diet and plant palatability are a consequence of the interaction between herbivores' ability to obtain and consume plants and external environments (Kimball & Provenza, 2003). The former may involve intra- and inter-specific competition, predation, and herbivores' attributes such as physiological adaptations and foraging strategies. The latter may include three main plant attributes: chemical characteristics of plants, physical characteristics of plants, and the availability of plants in the environment. For example, protein and fibers were important positive and negative chemical factors, respectively, in determining palatability of foods (Bucyanayandi & Bergeron, 1990; Rezsutek & Cameron, 2011). Plant secondary metabolites such as phenolics, tannins, alkaloids, and monoterpenes could also deter the consumption by herbivores (Barthelmess, 2001; Bergeron & Jodoin, 1987; Bucyanayandi & Bergeron, 1990; Goldberg *et al*., 1980; Hartley *et al*., 1995; Marquis

& Batzli, 1989; Takahashi & Shimada, 2008). Overall, while considering chemical characteristics of plants, both positive (e.g., proteins) and negative (e.g., plant secondary metabolites) factors need to be considered (Bergeron & Jodoin, 1987; Torregrossa & Dearing, 2009b). Second, the physical characteristics, such as toughness of plants can resist the consumption of herbivores (Hanley *et al*., 2007; Scheidel & Bruelheide, 1999). The physical characteristics of plants could be divided into many traits; such as tensile and shearing strength (Laca *et al*., 2001). The measurements of toughness represented the overall tissue strength of plants (Laca *et al*., 2001). Silica and lignin could deter the damage to plants caused by herbivores (Kimball & Provenza, 2003; Massey *at al*., 2007). It took longer time for herbivores to ingest and digest tough plant material, as a result, reduced the total intake of food (Laca *et al*., 2001). Third, as the availability of a plant species in the environment increases, the chances of the plant species being encountered and consumed by herbivores increase. Thus, other things being equal, the proportion of a plant in diets should increase with its relative abundance in the fields (Boyle *et al*., 2012). Ideally, all three plant attributes should be considered to better understand herbivore-plant interactions. However, most empirical studies focused on a single attribute. Few combined all plant attributes altogether. Finally, the characteristics of plants likely change with seasons, seasonal variation of diets and palatability should

be examined (López-Wilchis & Torres-Flores, 2007; Lindroth & Batzli, 1984).

Taiwan field vole (*Mircotus kikuchii*) is an endemic species in Taiwan, living in alpine meadows and fir forests, where Taiwan fir (*Abies kawakamii*) and Taiwan hemlock (*Tsuga chinensis* var. *formosana*) are dominant woody plants and Yushan cane (*Yushania niitakayamensis*) is dominant herbaceous plants (Chen, 1998). Taiwan field voles usually co-exist with two other rodent species, Formosan white-bellied rats (*Rattus culturatus*) and Formosan field mouse (*Apodemus semotus*) in the forests (Chang-Jen, 1997; Yeh, 2012). Lyu (1991) proposed that the reproductive cycles of voles were closely linked to their food resources, especially Yushan cane. Yeh (2012), using stable isotopes, found that the voles consumed more plants than other food resources in both alpine meadows and fir forests. Ho (2009) examined the palatability of thirteen plants to voles in alpine meadows, and found that *Yushania niitakayamensis* (玉山箭竹) and *Carex* spp. (薹屬) were the most palatable plants. The palatability could be explained by the abundance of plant species, and the percentage of hemicellulose they contained. Furthermore, Yeh *et al*. (2012) found that the preference of voles for different parts of Yushan cane varied with seasons, and vole's consumption facilitated the asexual reproduction (shooting) of Yushan canes. The above-mentioned studies have shown, in alpine meadows, the herbivory of Taiwan filed vole strongly

impacted the plants, and plant attributes did influence the foraging of voles. However, the relationship between voles and plants in fir forests remained unclear, given that the plant communities in the fir forests are dramatically different from that in the meadow.

The alpine ecosystems are expecting to see great changes because the global temperature has been proposed to increase in the following decades (Van Vuuren *et al.*, 2008). Understanding the relationship between plants and herbivores should allow us better predict the impacts of environmental changes. The purpose of this thesis was to: (1) understand the diets of voles in fir forests, and see if diet choice is consistent with plant palatability over seasons, and (2) test the palatability of five dominant plants to voles, and (3) examine the effects of plant attributes on palatability. I included all three plant attributes: chemical characteristics, physical characteristics, and abundance. The concept map of this thesis is shown in Fig. 1. Specifically, I aimed to test the following hypotheses:

Diets of Taiwan field voles

(1) Taiwan field voles forage selectively, and their diets change with seasons.

(2) Taiwan field vole diets reflect the palatability of plants.

Palatability of dominant plants to Taiwan field voles

(1) The palatability of different plant species differs, and the palatability within the

same plant species changes with seasons.

Plant attributes on palatability

(1) High palatability is associated with high nutrients and low digestion inhibitors.

(2) High palatability is associated with low toughness.

(3) High palatability is associated with high availability.

Materials and Methods

Study area

This study was conducted in a Taiwan Fir and Taiwan Hemlock mixed forest at the Hehuan Mountains (24°09’41.1”N, 121°17’10.4”E, 3005 m in altitude) of the Taroko National Park, Taiwan. The forest is nearby the High-Altitude Station of the Endemic Species Research Institute, Taiwan. The annual mean temperature was 7.0℃ and rainfall 366 mm (Yeh, 2012). Taiwan fir (*Abies kawakamii*, 台灣冷杉) and Taiwan hemlock (*Tsuga chinensis* var. *formosana*, 台灣鐵杉) are dominant woody plants, and Yushane cane (*Yushania niitakayamensis*, 玉山箭竹) is dominant herbaceous plant (Yeh, 2012).

On a 30 degree slope, I established an 11-by-11 sampling grid composed of 11 parallel lines (A to K), each with 11 trapping stations. The distances between lines and between stations were 10 meters. Trapping stations were marked with aluminum stakes. Line A was soon abandoned because it was at the edge of a cliff.

Field survey

Vegetation survey

To estimate the coverage of vegetation, 3 stations were randomly sampled along

the slope gradient of each grid line. Thirty stations were sampled in total. I randomly overlaid a 2-m-by-2-m frame on the ground, and estimated the percent coverage in area of each plant species within the frame. Vegetation was surveyed 3 times a year during vole trapping (see below).

Vole trapping

Vole trapping and vegetation survey were done in March, July, and November from July, 2011 to November, 2013, a total of 8 trapping sessions. Voles were trapped with a multiple-capture Ugglan special live trap (LxWxH=25-cm x 7.8-cm x 6.5-cm) and a squirrel cage (LxWxH=27-cm x 17-cm x 27-cm) at each station. Traps baited with sweet potato and oats mixed with peanut butter were serviced for five to six consecutive days. Traps were opened on the first evening, and checked twice in the morning and in the afternoon each day. Whenever a vole was captured, I collected its fresh fecal pellets immediately. Pellets were preserved in 70% alcohol and stored in a -80℃ refrigerator before diet analyses (see below). New individuals were marked with a fingerling ear tag. The following information was recorded: trapping station, ID, sex, body weight, reproductive condition (testes scrotal or abdominal for males; vaginal perforated or non-perforated for females). Adult voles (Male body weight ≧ 27 g; Female body

weight ≧ 26 g; Lyu, 1991) were brought back to the High-Altitude Station of the Endemic Species Research Institute for feeding trials (see below). All voles were released where they were captured after feeding trials.

Diet analyses

I followed the procedures used by several studies (Johnson *et al*., 1983; Lin & Lee, 2003), except that fecal samples were not sieved, to examine food fragments in fecal pellets to quantify vole diets. I first prepared reference images of the majority of plant species found at the study site. Preparation procedures were as follow: I collected aboveground parts of each plant species, separated leaves and stems, and treated them as different reference samples. Samples were cut into 0.5 cm fragments, and soaked in 95% warm alcohol to dissolve pigment. I then soaked samples in 3 N NaOH, and replaced NaOH daily until the samples were transparent that I could see epithelial cells clearly. I rinsed NaOH away with water, then preserved samples in 70% alcohol. I then took photographs of the epithelial cells through microscope.

I analyzed the fecal contents of 10 captured voles (randomly chosen) in each season. I first crumbled and homogenized fecal pellets of a vole in 70% alcohol with a glass rod. Three slides were made for each vole, and examined under a microscope with

400X magnification. For each slide, I looked for epithelial cells in 20 ocular fields, and took photographs of each field through microscope. There was a total of 60 (3x20) photographs per sample.

I compared the epithelial cells observed in the microscope field against the reference images of known plants to identify plant species consumed by voles. I recorded both the frequency and area of food items, including plant and animal fragments observed using the ImageJ 1.47v software. The five plant species, *Yushania niitakayamensis*, *Ainsliaea reflexa* (玉山鬼督郵), *Elatostema trilobulatum* (裂葉樓梯草), *Dryopsis transmorrisonensis* (玉山擬鱗毛蕨), and *Dicranum japonicum* (日本曲尾苔), tested in the feeding trials (see below) were particularly noted. Food items observed were identified to species if possible, then grouped into three categories: plants, insects and unknown (unidentifiable tissues or spores). Plant fragments were also further grouped into monocots (e.g., *Yushania niitakayamensis*), dicots (e.g., *Ainsliaea reflexa* and *Elatostema trilobulatum*), ferns (e.g., *Dryopsis transmorrisonensis*) and moss (e.g., *Dicranum japonicum*). The data from the 20 fields were pooled, and averaged over the 3 slides. The amount of each food item consumed by a vole was expressed as percentage based on the area of food items following the formula:

$$P_{ia} = (A_i / T) \times 100\%$$

P_{ia}: Percentage of *i* food item based on area

A_i: Area of *i* fragment

T: Sum of *i* fragment areas in the 20 microscope fields

Alternatively, the amount of each food item consumed by a vole was expressed as percentage based on the frequency of food items following the formula:

$$P_{ic} = (C_i / T) \times 100\%$$

P_{ic}: Percentage of *i* food item based on frequency (count)

C_i: Numbers of *i* food item counted

T: Sum of *i* fragments counted in the 20 microscope fields

Both calculated percentages gave the relative importance of a food item in the vole's diet (Hansson, 1970). Spores of fungi and ferns were excluded from analysis because they were too small to be compared with other fragments (Hung, 2002).

Palatability & feeding trials

The palatability of plants was measured as the amount of plant material consumed by voles over 12 hours. Trials were carried out over two years in three seasons: spring (3/21 – 4/7), summer (7/2 – 7/21) and autumn (11/12 – 12/1) in 2012; spring (3/23 – 4/11), summer (6/30 – 7/22) and autumn (11/05 – 11/24) in 2013 in the laboratory of the

High-Altitude Station of the Endemic Species Research Institute, Taiwan. Voles captured from the study area were immediately transported to and maintained in the laboratory under a 12-L:12-D light regime in ambient temperature. Voles were housed individually in standard rat cages (D47.0 x W25.5 x H21.5 cm^3) with 5-cm-thick aspen chip bedding (TAPVEI ®) for at least 5 days prior to the feeding trials to allow them accommodate to the housing environment. Water and food (fresh sweet potatoes and oats) were available *ad libitum* during this period. Females, if found pregnant, during the course of feeding experiment were excluded from further analyses because of their additional nutritional needs (Provenza *et al*., 2003).

The methods of feeding trials were adapted from the experimental protocols reported in previous researches (Batzli & Lesieutre, 1991; Marquis & Batzli, 1989; Ho, 2009). The top five dominant plants recorded in the vegetation survey (Table 1) were chosen as study targets. They were *Yushania niitakayamensis* (玉山箭竹), *Ainsliaea reflexa* (玉山鬼督郵), *Elatostema trilobulatum* (裂葉樓梯草), *Dryopsis transmorrisonensis* (玉山擬鱗毛蕨), and *Dicranum japonicum* (日本曲尾苔). Large overhead woody plants, including *Abies kawakamii* (台灣冷杉) and *Tsuga chinensis* var. *formosana* (台灣鐵杉) were not chosen for two reasons: First, their heights, exceed 10 meters on average, likely exclude accessibility by voles (Chen, 1998). Second, a

preliminary feeding trial indicates voles do not consume pine cones or pine seeds.

Upon the start of feeding trial, voles were moved to a new cage of the same size. Sheets of paper were used as bedding. Each vole was given one of the tested plant species per day for five consecutive days. The order of provision was random. The details follow. Each day, I collected fresh plant materials (aboveground parts; flowering buds and fruits were excluded) in the afternoon and soaked them in water to prevent dehydration. Before feeding trials, voles were weighed. Plant materials were dabbed dry with paper towel, and 15 g fresh plant materials were provided to each vole. To prevent plants from dehydration during trials, the plant stems or leaf petioles were wrapped in wet paper towels placed in a shallow dish. The voles were also given 15 g sweet potato and 8 g oats to assure that the consumption of a particular plant species was not affected by hunger (Kimball & Provenza, 2003), and that vole would not die from hunger (Ho, 2009). Water was provided *ad libitum*. Feeding trial lasted 12 hours, started from P.M. 8:00 and ended at A.M. 8:00.

After 12 hours, voles were weighed and moved to a new cage. Unconsumed plant materials, sweet potato and oats were carefully sorted and collected, dabbed dry with paper towels and weighted immediately. In order to control for the plant weight loss due to dehydration, a control cage with tested plant materials only were established during

feeding trails and weighed after 12 hours. The consumption of plant materials was calculated as below:

$$C = T_O \times (C_L / C_O) - T_L$$

C : Weight of plant material consumed

T_O: Weight of plant material offered in the beginning of the trial

T_L: Weight of plant material left at the end of the trial

C_O: Weight of control plant material in the beginning of the trial

C_L: Weight of control plant material at the end of the trial

The values of C were negative in some cases, probably because plant materials used in feeding trials and control cages differed in the relative amount of leaves, petioles, and stems. Nevertheless, the values were very small, I regarded it as no consumption (zero). The value of consumption was divided by the square root of tested vole's body weight to correct for the different metabolic requirements of animals of different sizes (Grodzinski & Wunder, 1975). They will be referred to as standardized palatability, hereafter.

Chemical analyses

Since it was not feasible to analyze all chemical compounds in plants, I chose to

analyze those compounds that were often associated with palatability, including dry matter, crude protein, neutral detergent fibers (NDF), acid detergent fibers (ADF), acid detergent lignin (ADL), ash, and total phenolics (Bergeron & Jodoin, 1987; Hartley *et al*., 1995; Marquis & Batzli, 1989). Fresh plants samples were collected in March, July and November in 2012 at the final day of feeding trials. Samples were put in plastic bags to prevent water loss and brought back to laboratory within 24 hours, freeze-dried immediately, and stored in -20℃ freezers before chemical analyses.

I followed standard methods described in related literatures to perform chemical analyses: dry matter (AOAC, 1984), ash (AOAC, 1984), crude protein (AOAC, 1984), neutral detergent fibers (NDF) (van Soest *et al*., 1991), acid detergent fibers (ADF) (Goering & van Soest, 1970), acid detergent lignin (ADL) (AOAC, 1984), and total phenolics (Velioglu *et al*., 1998). Detail procedures for analyzing each chemical compound are given in the Appendix 1. Nutritional contents (water, crude protein, neutral detergent fibers, acid detergent fibers, acid detergent lignin, and ash) were conducted in the laboratories of either Dr. Jih-Tay Hsu in the Department of Animal Science and Technology, National Taiwan University (NTU) or Dr. Han-Tsung Wang in the Department of Animal Science, Chinese Culture University (CCU). Total phenolics was done in the laboratory of Dr. Shaw-Yhi Hwang in the Department of

Entomology, National Chung Hsing University (NCHU).

Toughness analyses

Since the leaves, petioles and stems of plants were provided at the same time during trials, the measurements of toughness of different plant species depended on the part of plant consumed by voles during trials. Based on the consumption pattern, I measured the toughness of leaves in all tested plant species except *Dicranum japonicum*, which I measured stems. The measurement procedures follow: I stratified-random-sampled 10 stations, and collected three plants per species at each station. Plants were put in plastic bags individually to prevent water loss, brought back to laboratory immediately. Toughness was measured with a digital force gauge (Chatillon ® force measurement, DFE II series). Each plant was measured only once, the main vein was avoided during measurements. The values from the 30 plants were averaged. A preliminary study (in July 2013) showed that the toughness measured in the laboratory may increase slightly in all five plants (Table 22) likely due to water loss. Because I offered clipped plants to voles in the feeding trials, I used the toughness measured in the laboratory in the subsequent analyses.

Statistical analyses

I examined the normality and variance homogeneity of all data sets using Shapiro-Wilk and Levene's tests, respectively. Data sets that did not meet the assumptions of parametric statistical analyses were properly transformed to meet the assumptions. Otherwise, appropriate non-parametric statistical analyses or Markov chain Monte Carlo methods for Generalized Linear Mixed Models (MCMCglmm) would be applied.

First of all, I used a two-way ANOVA to examine the effects of sex and season (both as fix factors) on body weights of voles in feeding trials. I tested if the diet composition of voles changed with season by using a Chi-square test. The three main food categories: plants, invertebrates and unknown were then examined separately using the Kruskal-Wallis tests. I used MCMCglmm to run a two-way ANOVA to examine the effects of season and plant species on standardized palatability. Year was also put in as a random factor. I looked for the relationship between palatability and individual plant attributes: chemical compounds, toughness and relative abundance. I pooled together the data of standardized palatability and plant attributes from three seasons. Since the 7 chemical attributes measured were highly correlated with one another, I used a Principle Component Analysis to produce new independent variables (PCs). I used simple linear

regression to examine the relationship between palatability and each PC separately. I used MCMCglmm to run a one-way ANOVA to compare the toughness measured in the laboratory and in the field. A two-way ANOVA by MCMCglmm was performed to examine if toughness differed among plant species and seasons. I used a Pearson correlation to examine the relationship between the ranking in diet and the ranking in palatability. Statistical tests were performed by using the SAS 9.2 software, while MCMCglmm was performed by the R studio 3.0.2 software. Differences were considered statistically significant when $p < 0.05$.

Results

Field survey

Vegetation composition

The relative abundance of plant species was consistent among three seasons as shown by the percent coverage (Table 1). In general, *Yushania niitakayamensis* (玉山箭竹) was the most abundant plants in three seasons, followed by *Dicranum japonicum* (日本曲尾苔), *Elatostema trilobulatum* (裂葉樓梯草), *Dryopsis transmorrisonensis* (玉山擬鱗毛蕨) and *Anisliaea reflexa* (玉山鬼督郵). Although the latter two species were not recorded at sampling stations in March, 2012 (Table 1), field observation indicated that they were still present. The two species were patchily distributed. Overall, I recorded 46 species of plants in total, including 8 species of Bryophyta, 6 species of Pteridophyta, 2 species of Gymnosperms and 30 species of Angiosperms (including 13 monocots and 17 dicots) (Table 2). I collected the tissues of 38 species for making reference slides for the diet analyses.

Animals trapping

The numbers of voles that provided fecal samples in diet analysis or entered feeding trials are presented in Table 3. Fecal samples from ten adult voles were

randomly selected for diet analyses in each season. Some adult voles were trapped multiple times in different season/year. Although their fecal samples were collected multiple times, I only selected one of the samples for diet analysis. Forty-seven adult voles, 27 males and 20 females, were selected for feeding trials. Because of low population sizes in some seasons, a few voles were reused in different seasons. The body weights of voles entered feeding trails was 34.8±2.9 in male and 30.83±2.64 in female in March; 35.83±3.3 in male and 33.00±2.83 in female in July and 33.05±2.63 in male and 30.55±2.77 in female in November (Fig. 2). There was a significant difference between sexes in body weight (two-way ANOVA: $F = 12.25$; $p = 0.001$; Table 4), while there was no difference among seasons ($p = 0.07$). Other than Taiwan field voles, I captured many other vertebrates (Table 5) including 5 species of the order Rodentia: *Apodemus semotus* (台灣森鼠), *Niviventer culturatus* (高山白腹鼠), *Dremomys pernyi owstoni* (長吻松鼠) and *Tamiops maritimus formosanus* (條紋松鼠), 2 species of the order Soricomorpha: *Episoriculus fumidus* (台灣煙尖鼠) and *Anourosorex squamipes yamashinai* (山階氏鼬鼩), 2 species of the order Carnivora: *Mustela sibirica taivana* (華南鼬鼠) and *Mustela formosanus* (台灣小黃鼠狼), and 2 bird species *Garrulax morrisonianus* (金翼白眉) and *Fulvetta formosana* (褐頭花翼畫眉).

Diets of Taiwan field voles

Examining the relative importance of different food items in the vole's diet, either by area or count, over the three seasons, March, July, and November (Table 6-8), I found that plant was the most important food (95.3%, 91.5% and 92.2%, respectively), followed by unknown (3.1%, 5.9% and 6.8%, respectively) and insects (1.6%, 2.6% and 1.0%, respectively). The plant food in the diet was composed of 55.4% monocots (53.3% was *Yushania niitakayamensis*), 33.7% moss (0.2% was *Dicranum japonicum*), 5.2% dicots (1.1 % and 4.1% were *Ainsliaea reflexa* and *Elatostema trilobulatum*, respectively), and 0.4% of fern *Dryopsis transmorrisonensis* in March (Table 6). In July, the plant diet was composed of 70.7% monocots (all *Yushania niitakayamensis*), 16.2% moss (0.09% was *Dicranum japonicum*), 3.6% dicots (0.4% and 0.8% were *Ainsliaea reflexa* and *Elatostema trilobulatum*, respectively), and 1.0% of fern *Dryopsis transmorrisonensis* (Table 7). In November, the relative importance of monocots and moss were very similar to those in July. However, *Dicranum japonicum* increased to 2.8%, dicots decreased to 0.7%. Both dicots, *Ainsliaea reflexa* and *Elatostema trilobulatum*, and fern *Dryopsis transmorrisonensi* were not recorded in November (Table 8).

Basically voles did forage selectively since in many plant species the proportion of

a species in diets deviated from its relative abundance, although the two was positively correlated with each other (Fig. 3). Moreover, the diets of voles changed significantly with seasons (Chi-square test: $\chi^2 = 65.99$, $p < 0.001$, Table 9). By examining plant, invertebrate, and unknown separately (Table 10A), I found the seasonal difference was mainly contributed by the 'unknown' group. There was no significant differences among seasons in plant (Kruskal-Wallis test: U = 3.86, $p = 0.14$) and invertebrate (U = 0.66, $p = 0.72$, Table 10A) categories. The percentage of unknown food consumed was significantly different among seasons (U = 6.04; $p = 0.05$). Among the plant food items (Table 10B), I found there was significant differences among seasons in monocots (U = 5.86, $p = 0.05$) and moss (U = 7.51, $p = 0.02$). While there was no significant difference in dicots (U = 2.33, $p = 0.31$).

Palatability of dominant plants

A two-way ANOVA performed with MCMCglmm examining the effects of season and plant species on standardized palatability (Table 11 and 12) showed that there was a significant interaction between plant species and season (Table 13). The interaction occurred because the palatability of *Yushania niitakayamensis* (玉山箭竹) varied greatly among seasons, much higher in July than March and November ($p = 0.05$ in

March; p = 0.03 in November; Table 13, Fig. 4). Moreover, the palatability of different plant species was significantly different (p < 0.001; Table 13, Fig. 4). In general, *Yushania niitakayamensis* (玉山箭竹) was the most palatable plant to voles in three seasons, followed by *Elatostema trilobulatum* (裂葉樓梯草), *Anisliaea reflexa* (玉山鬼督郵), *Dryopsis transmorrisonensis* (玉山擬鱗毛蕨), and *Dicranum japonicum* (日本曲尾苔) (Table 13 and Fig. 4).

Effects of plant attributes on palatability

Effects of chemical characteristics of plants on palatability

The values of the 7 chemical attributes, including dry matter, crude protein, NDF (neutral detergent fiber), ADF (acid detergent fiber), ADL (acid detergent lignin), ash, and total phenolics for each plant species in March, July, and November are presented in Table 14-16, respectively. Because these attributes are highly correlated with one another (Table 19), I performed a Principle Component Analysis (PCA) to describe the overall chemical attribute of a plant (Table 17). The first three principle components (PC1 – PC3) were selected. Cumulatively, they explained over 93% of variation (Table 17). PC1 was significantly correlated with dry matter (+), crude protein (−), NDF (+) and ADF (+), ADL (+), ash (−) and total phenolics (+); PC2 was significantly

correlated with NDF (＋) and total phenolics (－); PC3 was significantly correlated with crude protein (＋) only (Table 19). Among the 3 PCs, only PC3 was significantly correlated with palatability (Simple linear regression: p = 0.04; R^2 = 0.30; Table 20C and Fig. 5) while PC1 and PC2 had no significant relationship with palatability (Simple linear regression: p = 0.07 for PC1; p = 0.14 for PC2; Table 20A and Table 20B, respectively). Therefore, high palatability was positively associated with crude protein (Table 19).

Effects of physical characteristics of plants on palatability

In most plant species, toughness measured in the laboratory and field were similar (two-way ANOVA by MCMCglmm: p = 0.72; Table 22), although the former was slightly higher than the latter (Fig. 6). The difference approached significance only in *Dicranum japonicum* (日本曲尾苔) (two-way ANOVA by MCMCglmm: p = 0.05; Table 22). I consistently used the toughness measured in the laboratory in all statistical analyses. Toughness of different plant species that measured in three seasons were shown in Table 21. There was a significant interaction between season and species (Table 23). The interaction occurred because the toughness of *Dicranum japonicum* (日本曲尾苔) varied greatly among seasons, low in March and high in November

(two-way ANOVA by MCMCglmm: $p < 0.001$ in March; $p < 0.001$ in November; Table 23 and Fig. 7). *Elatostema trilobulatum* (裂葉樓梯草) had the lowest toughness among all plant species, followed by *Yushania niitakayamensis* (玉山箭竹), *Anisliaea reflexa* (玉山鬼督郵), *Dryopsis transmorrisonensis* (玉山擬鱗毛蕨), and *Dicranum japonicum* (日本曲尾苔) (Table 23 and Fig. 7). There was a significant negative correlation between palatability and toughness (Simple linear regression: $p = 0.02$; $R^2 = 0.34$; Table 24 and Fig. 8), and suggested that high palatability was associated with low toughness.

Effects of abundance of plants on palatability

Relative abundance of plants was not correlated with standardized palatability, although the result approached significance (Simple linear regression: $p = 0.08$; $R^2 = 0.22$; Table 25 and Fig. 9).

Diet analyses and palatability of dominant plants

Vole diets come from plants with different relative abundance, while plant palatability is measured under controlled amount of plant. The more abundant a plant in the field, the more likely it will be encountered and consumed by voles. Thus, to examine the relationship between diets and palatability, one needs to control for the

relative abundance. To do so, I performed a simple linear regression between the percentage of different plants in diets and their relative abundance in the field (Simple linear regression: $p = 0.0001$; $R^2 = 0.69$; Table 26), and obtained the residuals of diets after accounting for abundance. Next, I correlated standardized palatability with the residuals. The results showed that there was a significant correlation between standardized palatability and diets (Pearson correlation: $p = 0.003$; Fig. 10).

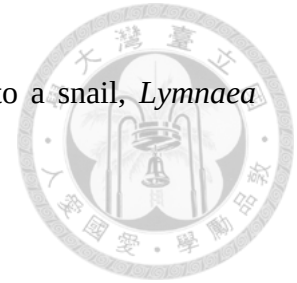
Discussion

The aim of this thesis is to understand the relationship between Taiwan field voles and dominant herbaceous plants in the Taiwan fir-Taiwan hemlock forest by combining diet analyses and palatability experiments. I first examined the hypothesis that voles foraged selectively, and their diets changed with seasons. The results showed that voles did not forage selectively based on the relationship between the proportion in diets and abundance of five plant species (Fig. 3). Furthermore, there was a significant overall seasonal effect in voles' diets (Table 9). Particularly, the unknown food items, but not plants or invertebrates (Table 10A), tended to be lower in March than July or November (Table 6–8). Unknown food items were mainly composed of spore-like tissues. It indicated that some food items associated with these spore-like tissues were quite important for voles in July and November. Dividing plants into specific categories, I found that the plant diets of voles were mainly monocots and moss. The consumption of these two food items together made up 88–90% of vole diets. The percentages changed with seasons as well (Table 10B). Voles consumed more moss in March (34% of diet), compared to July (16%) and November (17%). The *genus*, *Microtus*, has been found to prefer monocots over dicots in the field (López-Wilchis & Torres-Flores, 2007; Lindroth & Batzli, 1984), although monocots were sometimes overestimated and dicots

were underestimated (Alipayo *et al*., 1992). Indeed, the abilities that herbivores digest different plant species are different; resulting in quantifying the food fragments with bias. Nonetheless, from the vegetation survey I found that the coverage of monocots outmatched the coverage of dicots (Table 1); therefore, voles preferred to eat those that were abundant in the environment. Moss seemed to be another important food resource for voles in the forest. Previous studies have found that moss helped small mammals to persist in winter and adapted to a wider range of environments since they were available all year (Varner & Dearing, 2014). In this study, at least four species of moss were recorded in voles' diets (Table 6-8), the percentage of the unknown moss (M1), which was most likely *Pleurozium schreberi* (赤莖苔), remained the highest among all moss species. *Dicranum japonicum* (日本曲尾苔) was included in feeding trial since it was the most abundant moss from field observation and vegetation survey (Table 1). However, the results of diet analyses showed that voles consumed more M1 than *Dicranum japonicum* in the field. This indicates that voles showed selective foraging on moss. Fir, being too tall, was not considered a food item available to voles. Nevertheless, the fragments of fir epithelial cells were recorded once in diet analyses in March. Thus, voles may consume fir seedlings. Since there was only recorded once; fir is not likely a constant food resource to voles. On the other hand, fungi have been proposed to be an

important food resource for voles in the forest. Yeh (2012), at the same study site as mine, found that fungi made up 25% of vole diets in growing and non-growing seasons in forests. In my study, I also found that there were mycelia and spores of fungi in vole feces (especially in July). However, fungi were not included in diet analyses since they were too small to be properly quantified. Therefore, voles did consume fungi in the forest. Further investigation is required to know what species and how much were consumed by voles.

Second, I aimed to examine the hypothesis that different plants had different palatability, and the palatability within the same species changed with seasons. The results showed that different plants had significantly different palatability (Table 13). Across all seasons, *Yushania niitakayamensis* (玉山箭竹) was the most palatable plants to voles (Table 13 and Fig. 4). If herbivory pressure imposed by voles on a plant species depended on palatability, then *Yushania niitakayamensis* (玉山箭竹) would face the highest herbivory pressure. Since there was significant seasonal variation in palatability of *Yushania niitakayamensis* (Table 13 and Fig. 4), *Yushania niitakayamensis* likely faced different herbivory pressure in different seasons. Despite the seasonal variation in palatability; generally speaking, the palatability ranking of *Yushania niitakayamensis* remained stable across seasons (Table 11 and Table 12). It was consistent with a study



investigating the palatability of 8 freshwater macrophyte species to a snail, *Lymnaea stagnalis* (Elger & Barrat-Segretain, 2004).

Third, I examined how plant attributes affected the palatability of different plant species by testing the hypothesis that high palatability was associated with high nutrients and low digestion inhibitors. The results showed that only one plant chemical stood out—crude protein had a positive effect on palatability. Protein has been proposed as a nutrient which encouraged the consumption of food for herbivores (Cole & Batzli, 1979; Marquis & Batzli, 1989) since it is an important compound for animals to synthenize vital substances. I did not find the effects of negative chemical constituents, including fibers and phenolics. Fibers have been regarded as a negative compound since it reduced digestibility of plants to herbivores (Marquis & Batzli, 1989). Total phenolics are digestion inhibitors that herbivores avoided and deterred further consumption of plants (Marquis & Batzli, 1989). However, there was no significant negative correlation between either fibers or total phenolics and palatability in this study. I think it is likely Taiwan field voles have adapted physiologically to tackle them. Several previous study also suggested that herbivores were capable of adjusting to changing environments, particularly the changes in food quality because morphological, physiological and behavioral adaptations will take place (del Valle *et al*., 2006; Sassi *et al*., 2010;

Torregrossa & Dearing, 2009a). Therefore, it was possible that voles had adapted to specific chemical compounds that persisted in plants for a long time. Lovegrove (2010) compared the length of rodent intestines and found that herbivorous voles had large caecums and colons which indicated that voles were able to process plants with high fiber contents. Total phenolics could be divided into various secondary metabolites, such as tannins, lignins and flavonoids (Kimball and Provenza, 2003), different chemicals may have different effects on palatability (either levels or directions of effects). More detailed analyses of voles' abilities to cope with total phenolics are suggested.

Another hypothesis I examined is that high palatability is associated with low toughness. The results showed that not only different plants species had significantly different toughness, there was a significant interaction between plant species and seasons in toughness (Table 23 and Fig. 7). Low toughness of a plant was associated with higher palatability (Table 24), which was consistent with previous findings (e.g., Pennings & Paul, 1992). Laca *et al*. (2001) proposed that the measurement of toughness could be divided into tensile and shearing strength; accordingly, more detailed measurement on toughness were recommended. I also examined the hypothesis that high palatability is associated with high availability. The result showed that the relative

abundance was not significantly, though marginally (p=0.08), correlated with palatability (Table 25), which was inconsistent with the findings of Ho (2009). I only measured the palatability of 5 plant species. The small number of species, in comparison with 13 species in Ho (2009) may render the results insignificant. Particularly, there were many species of mosses in the study area (Table 2). Results of diet analyses suggested that at least 4 other moss species were part of voles' diets. *Dicranum japonicum* (日本曲尾苔) was the only one included simply because its relative abundance was the highest. If more moss species were included in the palatability experiments, probably the relationship between palatability and abundance would be much clearer.

In general, I found plant attributes (especially chemical and physical characteristics) affected palatability when they were examined separately. In order to know how all these plant attributes affected palatability altogether, I used cluster analysis and AIC model selection as tools. The cluster analysis included all plant characteristics (7 chemical compounds and toughness) except abundance to examine the similarity among plant species in each season. The results showed that *Yushania niitakayamensis* (玉山箭竹), *Anisliaea reflexa* (玉山鬼督郵) and *Elatostema trilobulatum* (裂葉樓梯草) were close to one another (Fig. 11), which were palatable plants (Fig. 4). *Dryopsis*

transmorrisonensis（玉山擬鱗毛蕨）and *Dicranum japonicum*（日本曲尾苔）were close each other (Fig. 11) (except for *Dicranum japonicum* in November) and they were unpalatable plant species (Fig. 4). The result of the cluster analysis indicated that particular combinations of plant characteristics would have higher palatability. I used AIC model selection to understand what combinations of plant characteristics contributed more to palatability. The results also showed that almost every plant characteristic was included (Table 27). Results of cluster analysis and model selection suggested that to completely understand how plant attributes affect palatability, every characteristic of plant should be considered.

Lastly, I examined the hypothesis that the diets of voles reflected the palatability of plants, and found that standardized diets and palatability matched perfectly (Fig. 10). Many other studies also found that diets were quite similar to palatability (reviewed in Batzli, 1985), although some studies found otherwise (e.g., Lantová & Lanta, 2008). The inconsistency is probably because diets were not standardized by relative abundance. Palatability is examined by feeding trials. They are non-choice experiments examining the intrinsic characteristics of a plant species. Whereas, diet analysis examines the consequence of a decision-making process in which herbivores encounter various plant species with drastically different relative abundance in the field. Therefore,

by standardizing the diets with relative abundance and then correlated with palatability was a better way to link these two parameters.

Both the results of diet analyses and palatability showed that *Yushania niitakayamensis* (玉山箭竹) was the most important food resource to Taiwan field voles across seasons in the fir forest. In alpine meadows, *Yushania niitakayamensis* (玉山箭竹) was also a critical food resource for voles (Ho, 2009). In addition, voles have been found that they prefer to consume different parts of *Yushania niitakayamensis* in different seasons (Yeh, 2010). Although voles seemed to be able to dwell in these two habitats all year, I found that forests were likely to be refuges in fall and winter for Taiwan field voles for two reasons: (1) Ho (2009) showed that in alpine meadows, the values of standardized palatability of *Yushania niitakayamensis* were 0.65, 0.75 and 0.44 in March, July and November, respectively. Note that there was a sharp decrease in November. In contrast, in this study I found the values of standardized palatability of *Yushania niitakayamensis* (玉山箭竹) were 0.74, 0.97 and 0.78 in March, July and November, respectively. There was no apparent decrease in November (Fig. 4). It indicated that the major food resource, *Yushania niitakayamensis* became unpalatable in November in meadows, but not in forests. It probably encouraged voles to move into forests in fall and winter to consume *Yushania niitakayamensis*. (2) In the study area,

Yeh (2012) found that vole population sizes were generally higher in meadows than in forests, except in fall and winter when population sizes were higher in forests than in meadows. Besides, number of vole captured in this study was also highest in November, lowest in July (Table 3). Based on these two reasons, I propose that forests are liable to be important habitats for Taiwan field voles in fall and winter. Nevertheless, it is possible that the population of voles in these two habitats are independent to each other, which means the increase and decrease of vole population are not due to the movement of voles between habitats. Accordingly, further research on whether voles will move to forests for wintering are required.

In conclusion, the results of diet analyses and palatability both showed that *Yushania niitakayamensis* (玉山箭竹) remained the most important food resource for Taiwan field voles in forests. Diets of voles and palatability of particular plants changed with seasons. The plant attributes did affect the palatability of plants to voles, especially crude protein and toughness. Results of diets and palatability were consistent with each other. Moreover, it seemed that forests were important habitats for voles in fall and winter since *Yushania niitakayamensis* was palatable all year round in forests. These results had shown that voles could impose strong herbivory pressure on vegetation in the forest, especially *Yushania niitakayamensis*.

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Tables

Table 1. Percent coverage in area of dominant plant species in the study site. The coverage (in %) was measured using a 2-m-by-2-m frame at each sampling station (N=30).

Species	November 2011	March 2012	July 2012	November 2012
Yushania niitakayamensis (玉山箭竹)	26.93	29.7	28.06	28.2
Dicranum japonicum (日本曲尾苔)	12.93	11.66	17.1	20.13
Abies kawakamii (台灣冷杉)	2.1	4.5	3	2.93
*Elatostema trilobulatum (*裂葉樓梯草)	1.53	1.03	2	1.06
Dryopsis transmorrisonensis (玉山擬鱗毛蕨)	0.23	0	0.43	0.7
Anisliaea reflexa (玉山鬼督郵)	0.06	0	0.5	0.46
Tsuga chinensis var. *formosana* (台灣鐵杉)	0.33	0.33	0.16	0
Platanthera brevicalcarata (短距粉蝶蘭)	0	0	0.56	0
Dryopteris reflexosquamata (逆鱗鱗毛蕨)	0.06	0.13	0.06	0.1
Ilex bioristsensis (苗栗冬青)	0.06	0.16	0	0.1
Dryopteris expansa (闊葉鱗毛蕨)	0	0.03	0.1	0
Coarse woody debris	3.16	6.7	4.9	5.36
Plant litter	52.5	45.73	43.1	40.93

Table 2. The species list of vegetation in the study area. Species that I made reference slides of are check-marked.

	Family Name	Species name	科名	植種名	Reference slides
苔類 Bryophyta	Dicranaceae	*Dicranum japonicum*	曲尾苔科	日本曲尾苔	V
		Dicranodontium denudatum		青毛苔	
	Hylocomiaceae	*Pleurozium schreberi*	塔苔科	赤莖苔	V
		Hylocomium splendens		塔苔	V
	Bryacceae	*Rhodobryum giganteum*	真苔科	暖地大葉苔	
	Sphagnaceae	*Sphagnum girgensohnii*	泥炭苔科	白齒泥炭苔	
	Brachytheciaceae	*Eurhynchium hians*	青苔科	美喙苔	
		Thuidium lepidoziaceum		細葉羽苔	
蕨類 Pteridophyta	Aspidiaceae	*Dryopsis transmorrisonensis*	三叉蕨科	玉山擬鱗毛蕨	V
	Dryopteridaceae	*Dryopteris reflexosquamata*	鱗毛蕨科	逆鱗鱗毛蕨	V
		Dryopteris expansa		闊葉鱗毛蕨	V
		Dryopteris lepidopoda		厚葉鱗毛蕨	V
		Polystichum stenophyllum		芽苞耳蕨	V

	Athyriaceae	*Athyrium reflexipinnum*	蹄蓋蕨科	逆羽蹄蓋蕨	
裸子植物 Gymnosperms	Pinaceae	*Abies kawakamii*	松科	台灣冷杉	V
		Tsuga chinensis var. *formosana*		台灣鐵杉	V
被子植物 Angiosperms 單子葉 Monocot	Poaceae	*Yushania niitakayamensis*	禾本科	玉山箭竹	V
		Aniselytron agrostoides		小穎溝稈草	V
	Araceae	*Arisaema consanguineum*	天南星科	長行天南星	V
	Liliaceae	*Paris polyphylla*	百合科	狹葉七葉一枝花	V
		Aletris formosana		台灣粉條兒菜	V
		Smilacina formosana		台灣鹿藥	V
	Smilacaceae	*Smilax vaginata*	菝葜科	薄葉菝契（玉山菝契）	V
		Smilax menispermoidea		巒大菝契	V

	Orchidaceae	*Platanthera brevicalcarata*	蘭科	短距粉蝶蘭	V
		Platanthera angustata		厚唇粉蝶蘭	V
		Goodyera nankoensis		南湖斑葉蘭	V
		Listera meifongensis		梅峰雙葉蘭	V
	Juncaceae	*Juncus triflorus*	燈心草科	玉山燈心草	V
雙子葉 (Dicot)	Compositae	*Ainsliaea reflexa*	菊科	玉山鬼督郵（台灣鬼督郵）	V
	Ericaceae	*Rhododendron pseudochrysanthum*	杜鵑花科	玉山杜鵑（森氏杜鵑）	V
	Urticaceae	*Elatostema trilobulatum*	蕁麻科	裂葉樓梯草	V
	Caprifoliaceae	*Lonicera acuminata*	忍冬科	阿里山忍冬（高山忍冬）	V
	Rosaceae	*Rubus pectinellus*	薔薇科	刺萼寒梅	V
	Ranunculaceae	*Ranunculus formosa-montanus*	毛茛科	蓬萊毛茛	
	Apiaceae	*Hydrocotyle nepalensis*	繖形花科	乞食碗	V

Polygonaceae	*Polygonum chinense*	蓼科	火炭母草（高山型）	
Pyrolaceae	*Cheilotheca humilis*	鹿蹄草科	水晶蘭	V
	Monotropa hypopithys		錫杖花	
	Chimaphila japonica		日本愛冬葉	V
Aquifoliaceae	*Ilex bioristsensis*	冬青科	苗栗冬青	V
Berberidaceae	*Berberis kawakamii*	小蘗科	台灣小蘗（川上氏小蘗）	V
Theaceae	*Eurya glaberrima*	山茶科	厚葉柃木	V
Thymelaeaceae	*Daphne morrisonesis*	瑞香科	玉山瑞香	V
Saxifragaceae	*Chrysosplenium lanuginosum*	虎耳草科	臺灣貓兒眼睛草	V
Oxalidaceae	*Oxalis acetosella*	酢醬草科	臺灣山酢醬草	

Table 3. Numbers of voles provided fecal samples in diet analyses and entered feeding trials.

Diet analyses			
	Male	Female	Total
March (Spring)	5	5	10 (23)
July (Summer)	6	4	10 (43)
November (Autumn)	3	7	10 (38)
Total	14	16	30 (104)
Feeding trials			
	Male	Female	Total
March (Spring)	10	6	16
July (Summer)	9	4	13
November (Autumn)	8	10	18
Total	27	20	47

Note: The data from 2012 and 2013 are pooled. Numbers in brackets represent the total fecal samples collected.

Table 4. Results of a two-way ANOVA that examined the effects of season and sex on body weight of voles used in feeding trials.

Source	DF	Type III SS	MS	F	*p*
Season	2	46.80	23.40	2.83	0.07
Sex	1	101.34	101.34	12.25	**0.001**
Season*Sex	2	4.63	2.32	0.28	0.76

Table 5. Vertebrates that were caught during vole trapping in the study area from June, 2011 to November, 2013.

Rodentia (嚙齒目)			
Family name	Species name	中文名	Note
Cricetidae (倉鼠科)	*Microtus kikuchii*	台灣高山田鼠	Endemic species
Muridae (鼠科)	*Apodemus semotus*	台灣森鼠	Endemic species
	Niviventer culturatus	高山白腹鼠	Endemic species
Sciuridae (松鼠科)	*Dremomys pernyi owstoni*	長吻松鼠	Endemic subspecies
	Tamiops maritimus formosanus	條紋松鼠	Endemic subspecies
Soricomorpha (鼩形目)			
Soricidae (鼩鼱科)	*Episoriculus fumidus*	台灣煙尖鼠(長尾鼩)	Endemic species
	Anourosorex squamipes yamashinai	山階氏鼩鼱(短尾鼩)	Endemic subspecies
Carnivora (食肉目)			
Mustelidae (貂科)	*Mustela sibirica taivana*	華南鼬鼠(黃鼠狼)	Endemic subspecies
	Mustela formosanus	台灣小黃鼠狼	Endemic species
Passeriformes (雀形目)			
Timaliidae (畫眉科)	*Garrulax morrisonianus*	金翼白眉(台灣噪眉)	Endemic species
	Fulvetta formosana	灰(褐)頭花翼畫眉	Endemic species

Table 6. The relative importance (in percentage) by area of different food items in the vole's diet in March (N=10). Values in brackets give the relative importance by count.

Items	Percentage	Items	Percentage	Species	Percentage
Plants	95.3 (95.6)	Monocot	55.4 (47.2)	YN	53.3 (46)
				MO	2.1 (1.2)
		Dicot	5.2 (2.1)	AR	1.1 (0.7)
				ET	4.1 (0.3)
		DT	0.4 (0.3)		
		Fir	0.5 (0.2)		
		Moss	33.7 (45.8)	M1	31 (41)
				DJ	0.2 (0.3)
				M3	0.9 (2.5)
				M4	0.4 (0.8)
				M	1.2 (1.2)
Insects	1.6 (1.2)				
Unknown	3.1 (3.2)				

Note: Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, DJ - *Dicranum japonicum* 日本曲尾苔, MO – unknown monocots, M to M4 represent unknown moss.

Table 7. The relative importance (in percentage) by area of different food items in the vole's diet in July (N=10). Values in brackets give the relative importance by count.

Items	Percentage	Items	Percentage	Species	Percentage
Plants	91.5 (81)	Monocot	70.7 (57.7)	YN	70.7 (57.7)
				MO	0
		Dicot	3.6 (2)	AR	0.4 (0.2)
				ET	0.8 (0.5)
		DT	1 (0.7)		
		Fir	0		
		Moss	16.2 (20.7)	M1	13.2 (16.2)
				DJ	0.09 (0.2)
				M3	0.09 (0.2)
				M4	2.5 (3.8)
				M	0.3 (0.3)
Insects	2.6 (1.8)				
Unknown	5.9 (17.2)				

Note: Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, DJ - *Dicranum japonicum* 日本曲尾苔, MO – Monocots, M to M4 represent unknown moss.

Table 8. The relative importance (in percentage) by area of different food items in the vole's diet in November (N=10). Values in brackets give the relative importance by count.

Items	Percentage	Items	Percentage	Species	Percentage
Plants	92.2 (87.8)	Monocot	74.7 (62.5)	YN	72.7 (61.5)
				MO	2 (1)
		Dicot	0.7 (0.3)	AR	0
				ET	0
		DT	0		
		Fir	0		
		Moss	16.9 (25)	M1	12.7 (20)
				DJ	2.8 (3)
				M3	0.2 (0.7)
				M4	0.3 (0.5)
				M	1 (0.8)
Insects	1.0 (0.8)				
Unknown	6.8 (11.4)				

Note: Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, DJ - *Dicranum japonicum* 日本曲尾苔, MO – Monocots, M to M4 represent unknown moss.

Table 9. Results of Chi-square tests that examined the effects of season on diet composition. The tests compared the occurrence frequencies of different food groups in different seasons.

	DF	Chi-square	*p*
Overall effects	4	65.99	**<0.001**
March v.s July	2	66.03	**<0.001**
July v.s November	2	11.07	**0.004**
March v.s November	2	29.94	**<0.001**

Table 10. The effect of season on diet composition based on the Kruskal-Wallis tests. Food items are categorized as (A) plant, invertebrate, or unknown. Plant food are further categorized as (B) monocot, dicot, or moss. The tests compared the areas of different food groups in different seasons.

(A)

Food	U	DF	*p*
Plant	3.86	2	0.14
Invertebrate	0.66	2	0.72
Unknown	6.04	2	**0.05**

(B)

Food	U	DF	*p*
Monocot	5.86	2	**0.05**
Dicot	2.33	2	0.31
Moss	7.51	2	**0.02**

Table 11. Standardized palatability of five dominant plants in March, July and November, in 2012 and 2013.

Year	2012 (N=10)	2013 (N=6)	2012 (N=4)	2013 (N=9)	2012 (N=8)	2013 (N=10)
Month	March	March	July	July	November	November
玉山箭竹	0.72±0.38	0.79±0.30	0.94±0.32	0.99±0.23	0.84±0.31	0.74±0.23
玉山鬼督郵	0.47±0.23	0.53±0.1	0.53±0.20	0.47±0.19	0.56±0.23	0.52±0.15
裂葉樓梯草	0.35±0.17	0.40±0.09	0.44±0.17	0.64±0.31	0.64±0.28	0.52±0.33
玉山擬鱗毛蕨	0.26±0.21	0.12±0.09	0.19±0.17	0.21±0.11	0.24±0.03	0.26±0.17
日本曲尾苔	0.09±0.15	0.24±0.15	0.07±0.14	0.16±0.25	0.43±0.29	0.14±0.20

Note: Values are calculated as consumed plant weight / square root of vole body weight.

Table 12. Ranking in standardized palatability of five dominant plants in March, July and November, in 2012 and 2013.

	2012 (N=10)	2013 (N=6)	2012 (N=4)	2013 (N=9)	2012 (N=8)	2013 (N=10)	Total N=47
	March	March	July	July	November	November	Overall
玉山箭竹	+++++	+++++	+++++	+++++	+++++	+++++	+++++
玉山鬼督郵	++++	++++	++++	+++	+++	+++	++++
裂葉樓梯草	+++	+++	+++	++++	++++	++++	+++
玉山擬鱗毛蕨	++	+	++	++	+	++	++
日本曲尾苔	+	++	+	+	++	+	+

Note: The number of + sign indicates the degree of palatability.

Table 13. Results of a two-way ANOVA using MCMCglmm that examined the effects of season and species on standardized palatability. The mean indicates the strength and direction of the main effects and the combined effects in the interaction. Values are standardized palatability.

Parameter	mean	95% CI	pMCMC
Intercept (July, AR)	0.49	0.38 to 0.63	**0.003**
Season (July→March)	0.00009	-0.17 to 0.16	0.99
Season (July→November)	0.05	-0.11 to 0.21	0.60
Species (AR→DJ)	-0.36	-0.53 to -0.18	**<0.001**
Species (AR→DT)	-0.29	-0.46 to -0.11	**0.003**
Species (AR→ET)	0.09	-0.09 to 0.26	0.29
Species (AR→YN)	0.48	0.31 to 0.65	**<0.001**
Season*Species (March, DJ)	0.01	-0.21 to 0.25	0.89
Season*Species (November, DJ)	0.09	-0.15 to 0.31	0.45
Season*Species (March, DT)	-0.02	-0.23 to 0.22	0.99
Season*Species (November, DT)	0.00001	-0.22 to 0.25	0.99
Season*Species (March, ET)	-0.22	-0.46 to 0.007	0.08
Season*Species (November, ET)	-0.06	-0.27 to 0.17	0.63
Season*Species (March, YN)	-0.23	-0.46 to -0.10	**0.05**
Season*Species (November, YN)	-0.23	-0.44 to 0.01	**0.03**

Note: Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, DJ - *Dicranum japonicum* 日本曲尾苔.

Table 14. Chemical attributes of plants (aboveground parts) in March, 2012.

Species	Dry matter (%)	Crude protein (DM%)	NDF (DM%)	ADF (DM%)	ADL (DM%)	Ash (DM%)	Total phenolics (DM%)
玉山箭竹	48.43	13.38	76.86	47.25	11.90	10.96	1.33
玉山鬼督郵	23.37	9.00	36.24	31.29	3.85	9.97	1.13
裂葉樓梯草	17.06	16.38	36.57	22.74	3.97	13.28	0.64
玉山擬鱗毛蕨	34.08	8.08	58.66	47.02	21.71	4.41	4.81
日本曲尾苔	24.21	6.47	78.10	53.00	10.23	3.38	1.37

Table 15. Chemical attributes of plants (aboveground parts) in July, 2012.

Species	Dry matter (%)	Crude protein (DM%)	NDF (DM%)	ADF (DM%)	ADL (DM%)	Ash (DM%)	Total phenolics (DM%)
玉山箭竹	37.77	15.67	78.67	37.30	6.13	8.99	0.97
玉山鬼督郵	18.17	10.02	34.53	32.89	4.52	9.45	1.03
裂葉樓梯草	12.10	14.67	29.23	24.97	2.86	15.73	0.88
玉山擬鱗毛蕨	26.72	9.81	54.86	49.16	21.08	5.18	2.84
日本曲尾苔	54.28	5.71	76.41	46.19	7.42	3.45	0.85

Table 16. Chemical attributes of plants (aboveground parts) in November, 2012.

Species	Dry matter (%)	Crude protein (DM%)	NDF (DM%)	ADF (DM%)	ADL (DM%)	Ash (DM%)	Total phenolics (DM%)
玉山箭竹	42.00	16.23	81.79	38.20	7.63	10.30	1.69
玉山鬼督郵	14.63	13.93	33.44	22.57	3.73	16.10	1.18
裂葉樓梯草	23.19	9.47	34.16	31.49	4.25	10.31	0.9
玉山擬鱗毛蕨	28.63	7.98	81.48	44.00	7.77	3.77	3.06
日本曲尾苔	34.22	11.82	54.49	39.59	17.85	5.46	0.7

Table 17. Results of Principle Component Analysis.

	Eigenvalue	Difference	Proportion	Cumulative
PC1	4.08	2.69	0.58	0.58
PC2	1.40	0.36	0.20	0.78
PC3	1.03	0.75	0.15	0.93
PC4	0.28	0.17	0.04	0.97
PC5	0.11	0.04	0.02	0.99

Table 18. Eigenvectors of the Principle Components.

	Eigenvectors				
	PC1	PC2	PC3	PC4	PC5
Dry Matter	0.34	0.43	0.32	-0.75	0.03
Crude Protein	-0.30	0.10	0.75	0.32	-0.17
NDF	0.36	0.51	0.21	0.42	-0.18
ADF	0.47	0.09	-0.06	0.29	0.60
ADL	0.39	-0.43	0.29	0.13	0.25
Ash	-0.45	-0.008	0.31	-0.15	0.67
Phenolics	0.30	-0.60	0.32	-0.18	-0.26

Table 19. Correlation matrix of 7 chemical compounds and three principle components. The statistical significance (p values) for each coefficient was given below each coefficient.

Pearson Correlation Coefficients, N = 15										
Prob > |r| under H0: Rho=0										
	Dry Matter	Crude Protein	NDF	ADF	ADL	Ash	Phenolics	PC1	PC2	PC3
Dry Matter	1	-0.16	0.78	0.63	0.36	-0.50	0.19	0.69	0.51	0.33
		0.56	**0.0006**	**0.01**	0.19	0.06	0.49	**0.005**	0.05	0.23
Crude Protein	-0.16	1	-0.17	-0.59	-0.29	0.75	-0.22	-0.60	0.12	0.77
	0.56		0.54	**0.02**	0.29	**0.001**	0.43	**0.02**	0.67	**0.0009**
NDF	0.78	-0.17	1	0.77	0.33	-0.62	0.08	0.73	0.60	0.21
	0.0006	0.54		**0.0009**	0.23	**0.01**	0.77	**0.002**	**0.02**	0.45
ADF	0.63	-0.59	0.77	1	0.70	-0.86	0.45	0.96	0.11	-0.06
	0.01	**0.02**	**0.0009**		**0.004**	**<0.0001**	0.09	**<0.0001**	0.69	0.83
ADL	0.36	-0.29	0.33	0.70	1	-0.62	0.89	0.79	-0.51	0.29
	0.19	0.29	0.23	**0.004**		**0.01**	**<0.0001**	**0.0005**	0.05	0.29
Ash	-0.50	0.75	-0.62	-0.86	-0.62	1	-0.44	-0.91	-0.01	0.31
	0.06	**0.001**	**0.01**	**<0.0001**	**0.01**		0.10	**<0.0001**	0.97	0.25
Phenolics	0.19	-0.22	0.08	0.45	0.89	-0.44	1	0.60	-0.70	0.32
	0.49	0.43	0.77	0.09	**<0.0001**	0.10		**0.02**	**0.003**	0.24

Table 20. Simple linear regression of standardized palatability and (A) PC1, (B) PC2, and (C) PC3.

(A)

Analysis of Variance						
Source	DF	SS	MS	F	R-square	*p*
Model	1	0.21	0.21	3.8	0.23	0.07
Error	13	0.70	0.05			
Corrected Total	14	0.91				

(B)

Analysis of Variance						
Source	DF	SS	MS	F	R-square	*p*
Model	1	0.14	0.14	2.42	0.16	0.14
Error	13	0.77	0.06			
Corrected Total	14	0.91				

(C)

Analysis of Variance						
Source	DF	SS	MS	F	R-square	*p*
Model	1	0.27	0.270	5.53	0.30	**0.04**
Error	13	0.64	0.05			
Corrected Total	14	0.91				

Table 21. Toughness (in grams) of five dominant plants measured in the laboratory in three seasons.

Seasons	Species	Mean	SD
March	玉山箭竹	86.40	7.61
	玉山鬼督郵	95.80	15.55
	裂葉樓梯草	43.73	5.85
	玉山擬鱗毛蕨	161.50	21.14
	日本曲尾苔	135.03	23.70
July	玉山箭竹	92.40	7.58
	玉山鬼督郵	93.03	17.56
	裂葉樓梯草	49.63	8.76
	玉山擬鱗毛蕨	175.93	34.88
	日本曲尾苔	237.90	114.30
November	玉山箭竹	101.73	14.17
	玉山鬼督郵	87.40	14.20
	裂葉樓梯草	51.30	9.46
	玉山擬鱗毛蕨	203.27	30.27
	日本曲尾苔	341.80	86.78

Table 22. Results of a two-way ANOVA using MCMCglmm that examined the effects of species and location (laboratory and field) on toughness. The mean indicates the strength and direction of the main effects and the combined effects in the interaction. Values are toughness (g).

Parameter	mean	95% CI	pMCMC
Intercept (AR, Lab)	92.46	67.03 to 115.68	**<0.001**
Species (AR→DJ)	145.44	110.16 to 180.33	**<0.001**
Species (AR→DT)	83.39	46.88 to 116.94	**<0.001**
Species (AR→ET)	-42.14	-79.39 to -7.92	**0.02**
Species (AR→YN)	-0.15	-35.19 to 37.60	0.97
Site (Lab→field)	-6.21	-42.61 to 27.60	0.72
Species*Site (DJ, field)	-52.41	-104.64 to 0.35	**0.05**
Species*Site (DT, field)	-23.07	-73.58 to 28.08	0.37
Species*Site (ET, field)	2.41	-52.74 to 47.40	0.90
Species*Site (YN, filed)	6.07	-49.85 to 51.61	0.80

Note: Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, DJ - *Dicranum japonicum* 日本曲尾苔.

Table 23. Results of a two-way ANOVA using MCMCglmm that examined the effects of species and season on toughness. The mean indicates the strength and direction of the main effects and the combined effects in the interaction. Values are toughness (g).

Parameter	mean	95% CI	pMCMC
Intercept (AR, July)	93.11	68.68 to 119.80	**<0.001**
Species (AR→DJ)	144.63	106.00 to 178.06	**<0.001**
Species (AR→DT)	83.21	46.21 to 116.85	**<0.001**
Species (AR→ET)	-42.98	-78.68 to -5.96	**0.02**
Species (AR→YN)	-0.59	-35.43 to 34.50	0.98
Seasons (July→March)	2.83	-32.62 to 37.68	0.87
Seasons (July→November)	-5.93	-39.55 to 30.68	0.74
Species*Seasons (DJ, March)	-105.45	-156.45 to -58.18	**<0.001**
Species*Seasons (DT, March)	-17.51	-71.33 to 30.74	0.50
Species*Seasons (ET, March)	-9.76	-59.74 to 40.40	0.67
Species*Seasons (YN, March)	-9.04	-63.10 to 35.23	0.75
Species*Seasons (DJ, November)	109.87	61.07 to 160.92	**<0.001**
Species*Seasons (DT, November)	32.46	-15.65 to 80.28	0.21
Species*Seasons (ET, November)	9.87	-36.55 to 63.33	0.70
Species*Seasons (YN, November)	15.45	-33.71 to 64.88	0.54

Note: Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, DJ - *Dicranum japonicum* 日本曲尾苔.

Table 24. Simple linear regression of standardized palatability and toughness.

Analysis of Variance						
Source	DF	SS	MS	F	R-square	*p*
Model	1	4.74	4.74	6.65	0.34	**0.02**
Error	13	9.26	0.71			
Corrected Total	14	14				

Table 25. Simple linear regression of standardized palatability and relative abundance.

Analysis of Variance						
Source	DF	SS	MS	F	R-square	*p*
Model	1	3.04	3.04	3.63	0.22	0.08
Error	13	10.91	0.84			
Corrected Total	14	13.96				

Table 26. Simple linear regression of relative abundance and diets of five plant species in three seasons.

Analysis of Variance						
Source	DF	SS	MS	F	R-square	*p*
Model	1	9.59	9.59	28.51	0.69	**0.0001**
Error	13	4.37	0.34			
Corrected Total	14	13.96				

Table 27. Results of model selection. Dependent variable y = standardized palatability; independent variables are x1 = dry matter, x2 = crude protein, x3 = NDF, x4 = ADF, x5 = ADL, x6 = Ash, x7 = total phenolics, x8 = toughness, x9 = relative abundance.

Number in Model	Adjusted R-Square	R-Square	AIC	BIC	SBC	SSE	Variables in Model	delta AIC
8	0.88	0.95	-68.52	-39.75	-62.15	0.05	x1 x2 x3 x4 x6 x7 x8 x9	0
7	0.88	0.94	-67.93	-47.21	-62.27	0.06	x1 x3 x4 x6 x7 x8 x9	0.59
8	0.88	0.94	-67.11	-41.19	-60.73	0.05	x1 x3 x4 x5 x6 x7 x8 x9	1.41
9	0.86	0.95	-67.13	-33.13	-60.05	0.05	x1 x2 x3 x4 x5 x6 x7 x8 x9	1.39
5	0.86	0.91	-65.80	-57.22	-61.55	0.08	x1 x3 x5 x7 x9	2.72
6	0.85	0.91	-64.89	-53.72	-59.93	0.08	x1 x3 x5 x7 x8 x9	3.64

Figures

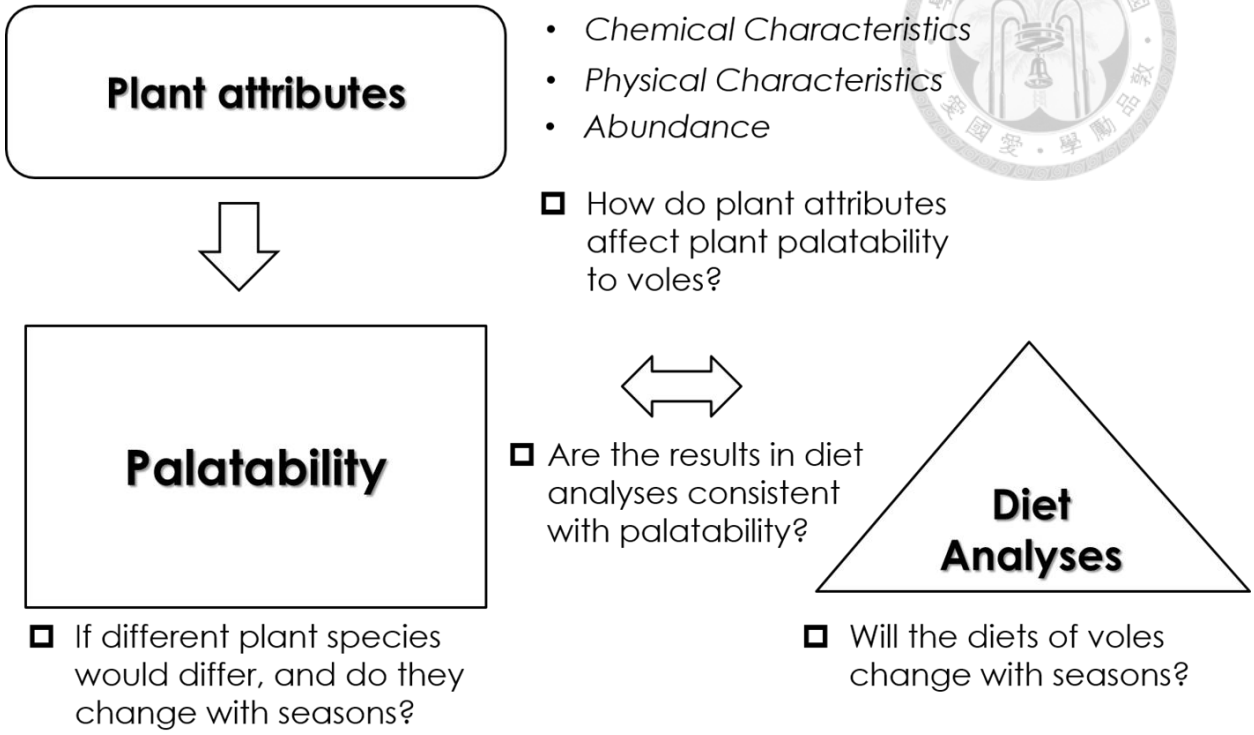


Figure 1. The concept map of this thesis.

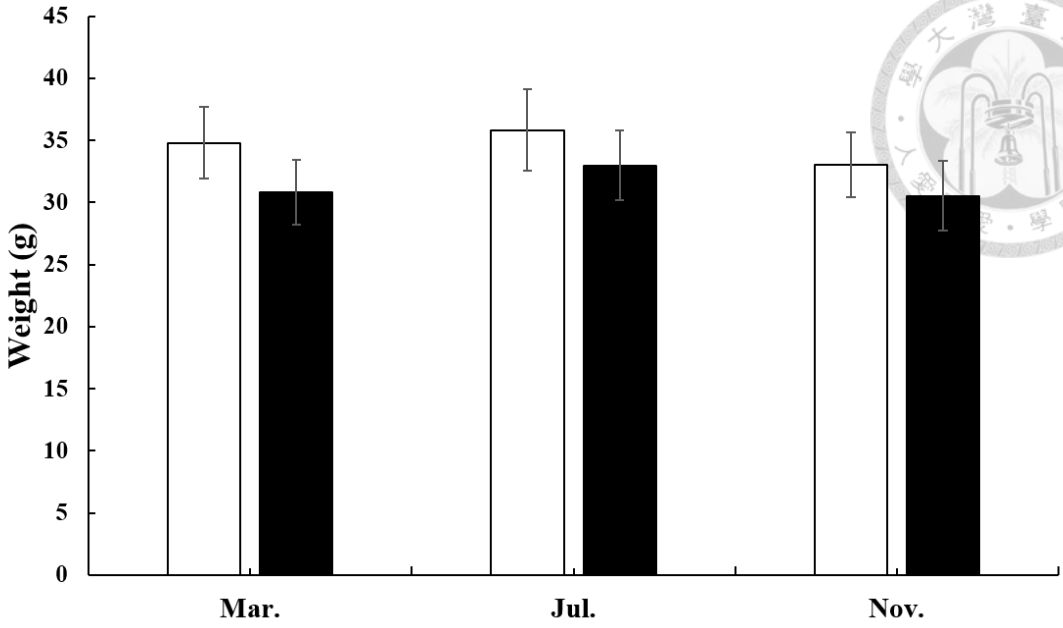


Figure 2. Sexual difference in body weight (mean±1sd) of voles (□ for male vs. ■ for female) that used in feeding trials in three seasons (March: n = 10 for male, n = 6 for female; July: n = 9 for male, n = 4 for female; November: n = 8 for male, n = 10 for female). The body weights of male voles were significantly higher than those of females (two-way ANOVA: F = 12.25; p = 0.001).

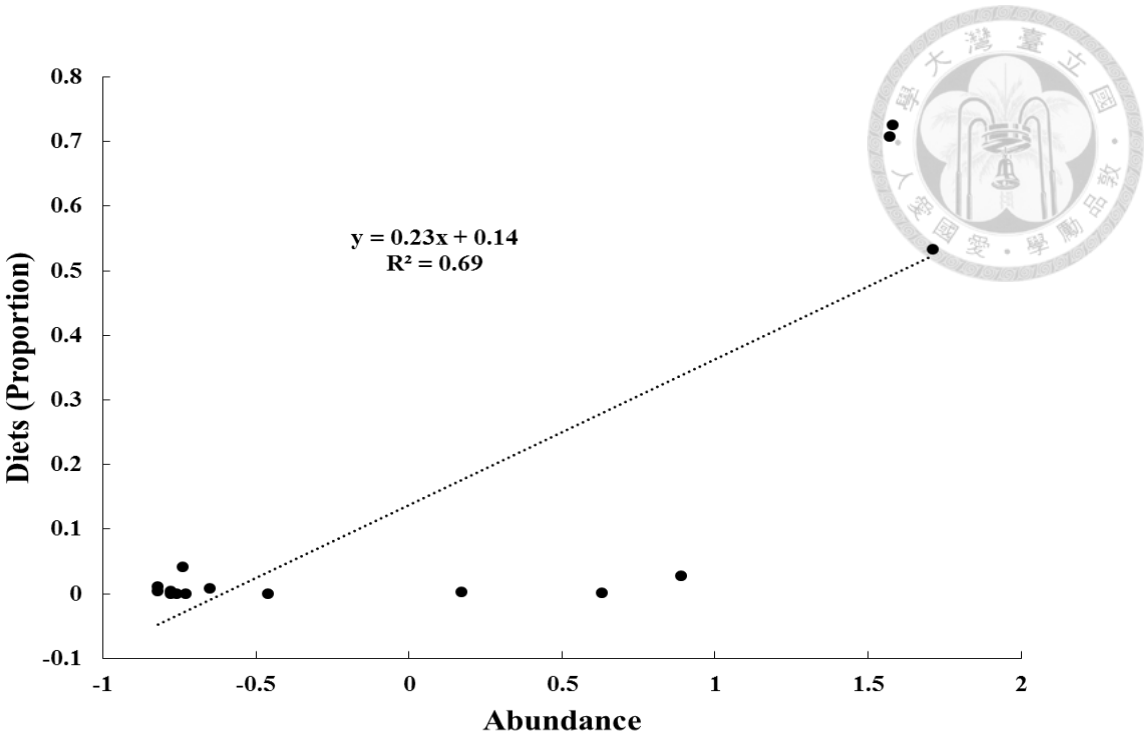


Figure 3. The relationship between diets and relative abundance of five tested plants.

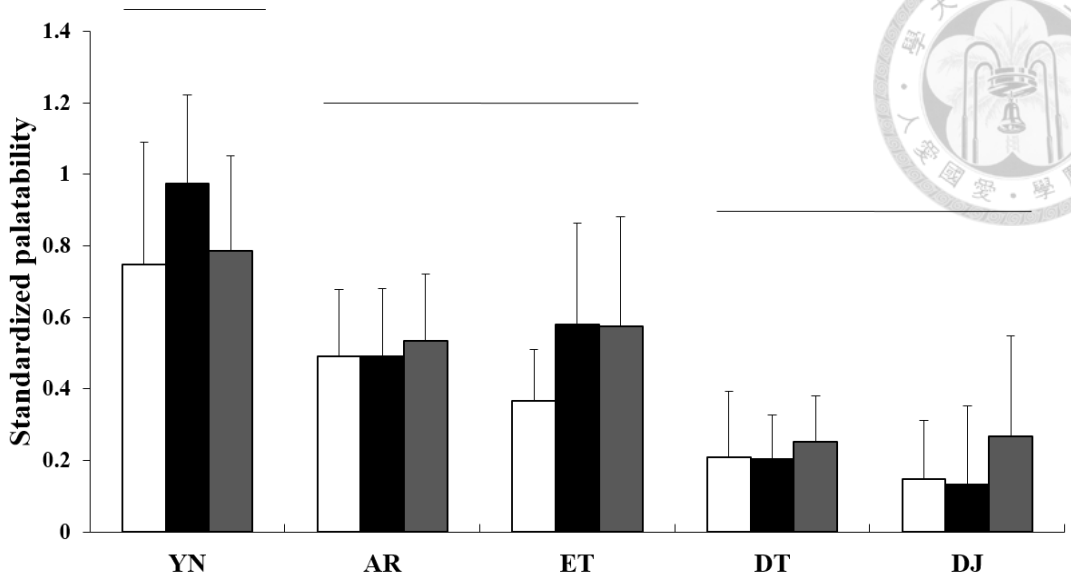


Figure 4. Standardized palatability (mean±1sd) of five dominant plants in March (□, *n* = 16), July (■, *n* = 13), November (■, *n* = 18). Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, and DJ - *Dicranum japonicum* 日本曲尾苔.

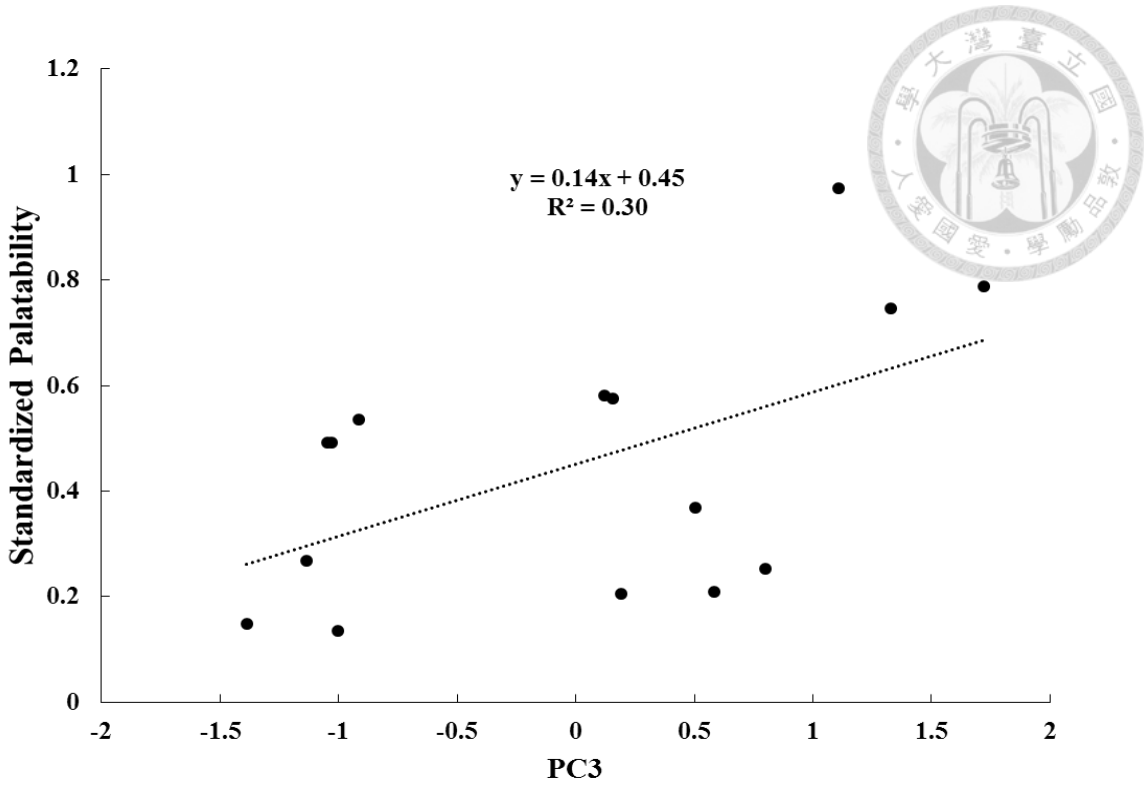


Figure 5. Simple linear regression of standardized palatability and PC3 (F = 5.53; p = 0.04).

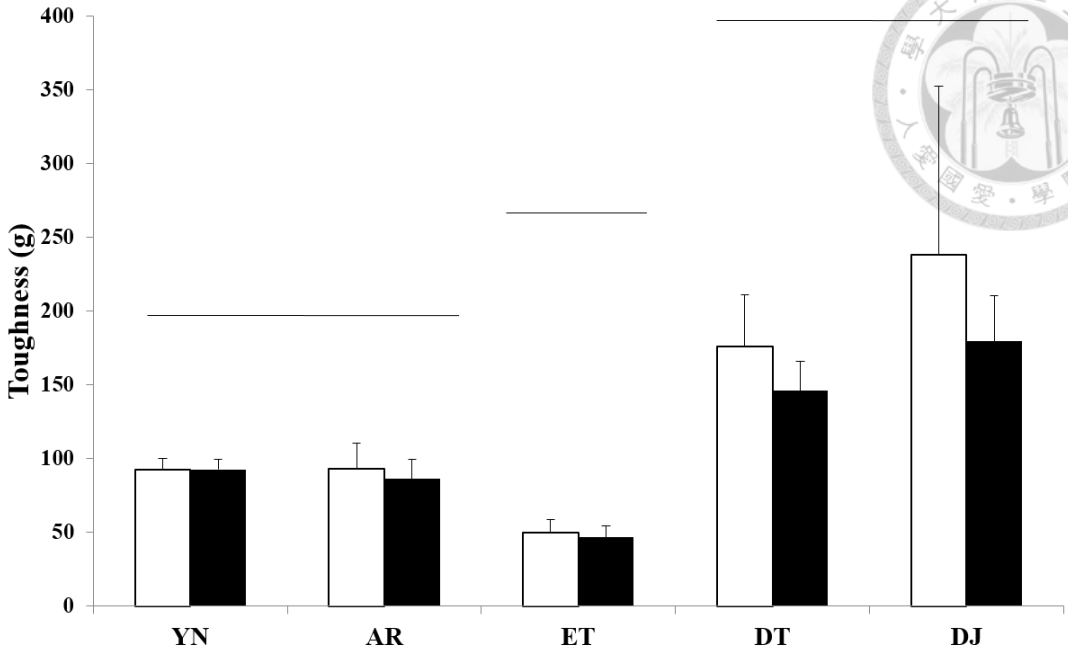


Figure 6. Mean (±1SD) toughness of five dominant plants that measured in laboratory (□, *n* = 10) and field (■, *n* = 10). Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, and DJ - *Dicranum japonicum* 日本曲尾苔.

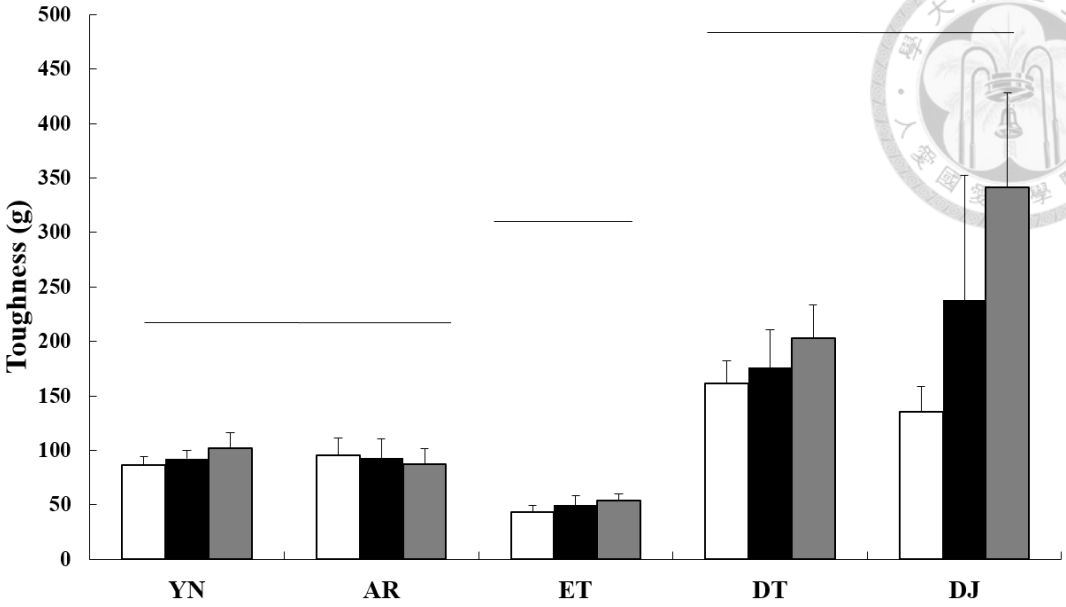


Figure 7. Mean (±1SD) toughness of five dominant plants that measured in laboratory in March (□, *n* = 10), July (■, *n* = 10), and November (■, *n* = 10). Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, and DJ - *Dicranum japonicum* 日本曲尾苔.

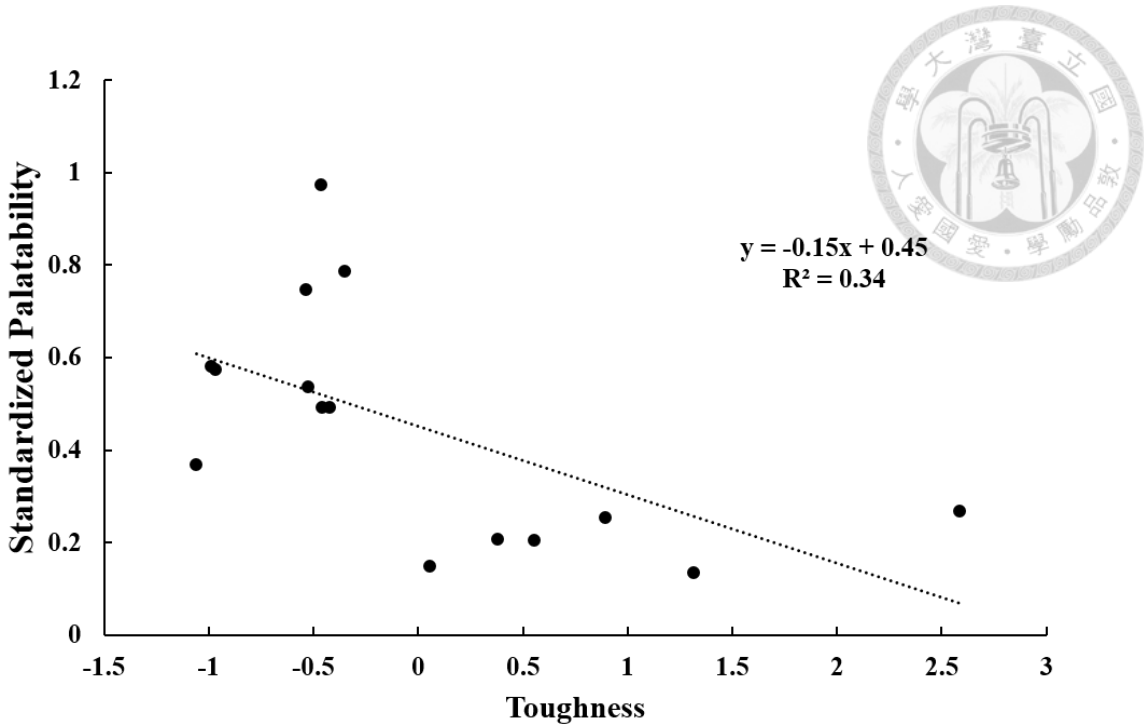


Figure 8. Simple linear regression of standardized palatability and toughness (F = 6.65; p = 0.02).

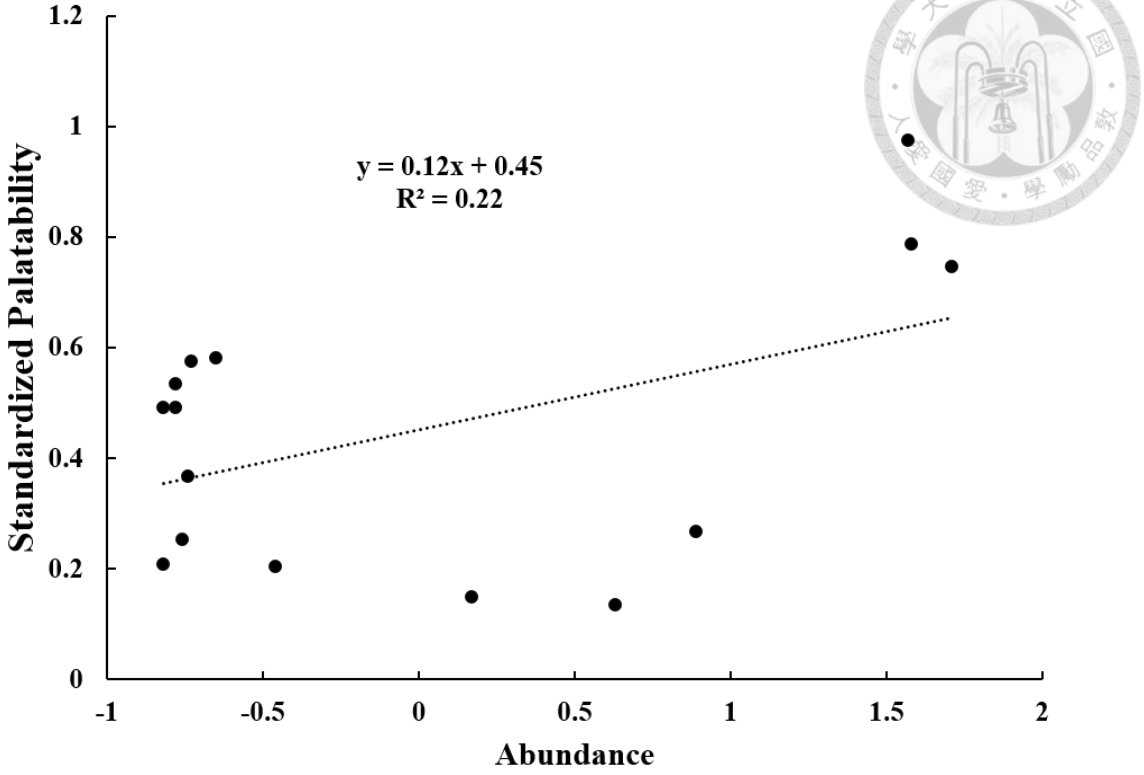


Figure 9. Simple linear regression of standardized palatability and abundance (F = 3.63; p = 0.08).

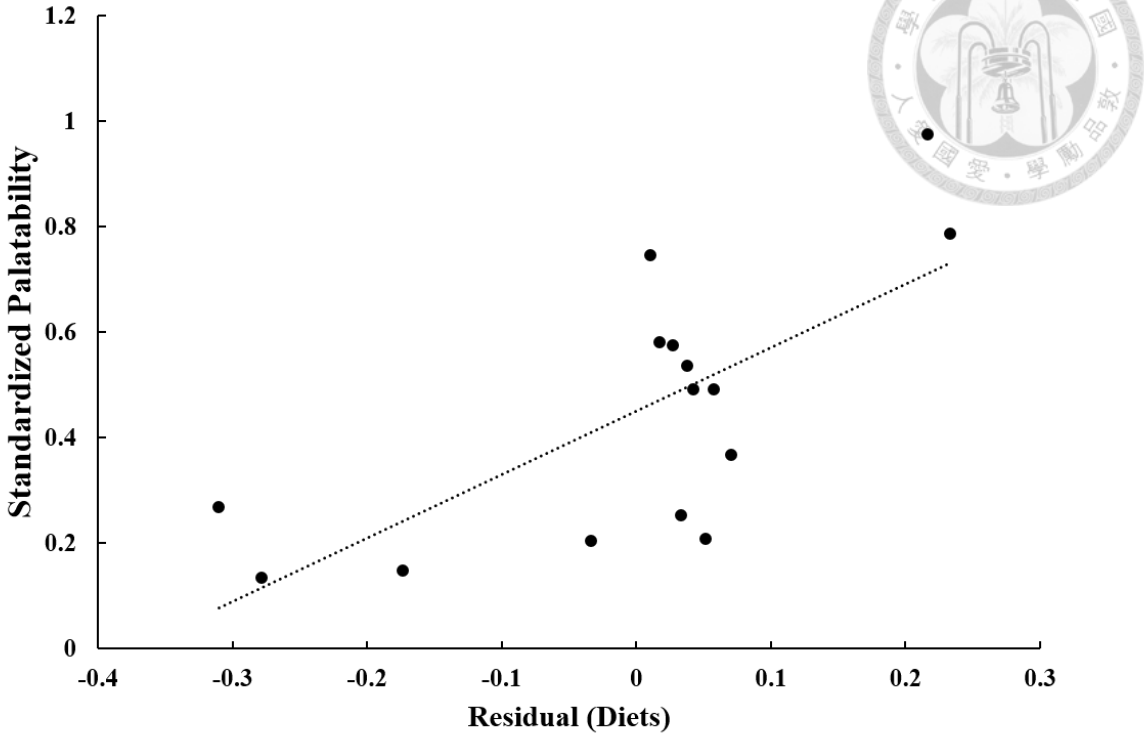


Figure 10. Relationship between standardized palatability and diets after accountng for availability (Pearson correlation: $r = 0.72$; $p = 0.003$).

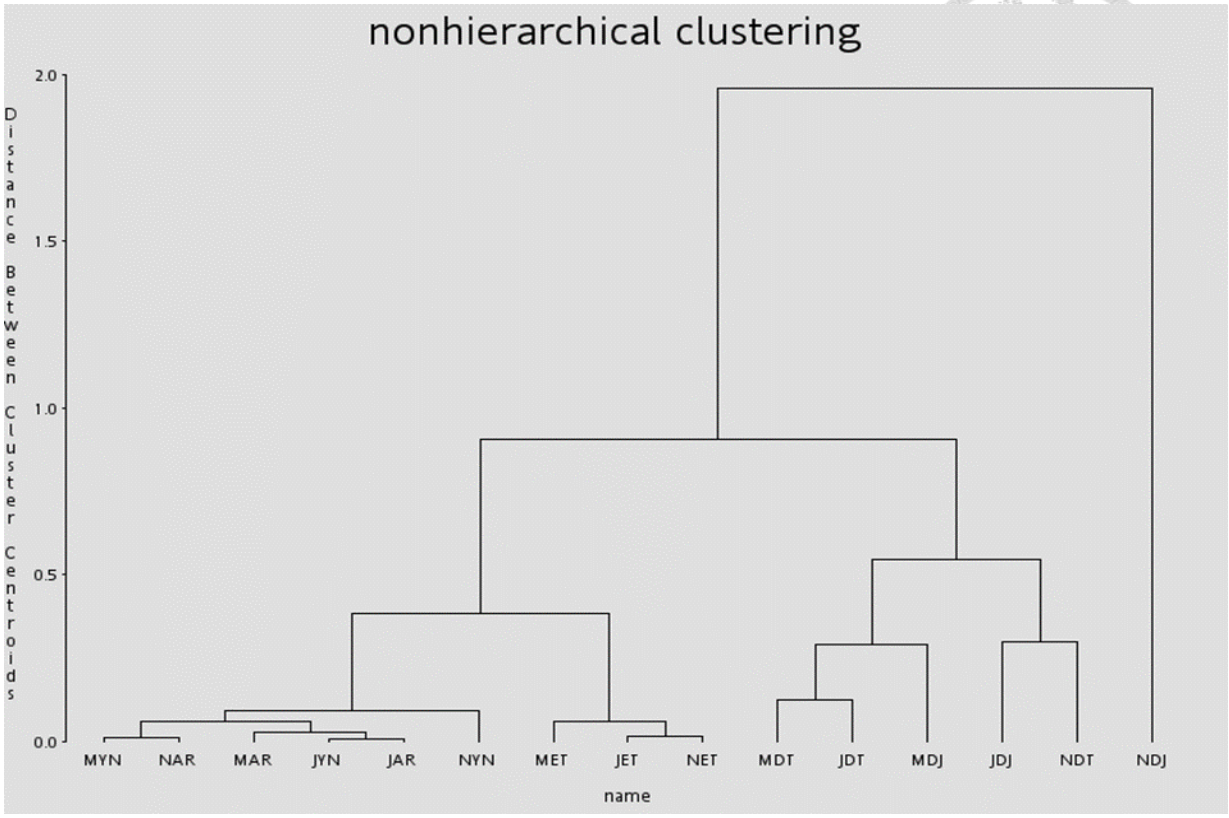


Figure 11. Result of cluster anaylsis by centroids hierarchical method. Plant attributes were all included (7 chemical compounds and toughness); plants were combined if they were similar in these characteristics. Abbreviation for YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, and DJ - *Dicranum japonicum* 日本曲尾苔.

Appendix

Appendix 1. Methods of chemical analysis

Appendix 1.1. 乾物質(Dry matter)分析方法(AOAC, 1984)：

1. 將 1 g 的樣品置於烘箱當中，以 110℃烘乾水分，每隔兩小時秤重，直到所測的重量恆定為止
2. 剩下的重量除以原重量即為乾物重

Appendix 1.2. 灰份(ash)分析方法(AOAC, 1984)：

1. 將樣品(0.5 g)置於灰化爐中，以 600℃，將樣品灰化呈灰色粉末為止
2. 將剩餘的灰色粉末秤重，並除以原重量即為灰份

Appendix 1.3. 粗蛋白(Crude protein)分析方法(AOAC, 1984)：

1. 取樣品 0.5 g 用秤紙包起來，分別放入 200 mL 的凱氏氮分解瓶當中
2. 每管加入一顆消化錠(卡達爾片劑，Merck)並加入 20 mL 濃硫酸以及沸石
3. 將瓶子放到分解裝置當中加熱。先以 10 預熱，接著再以 7~8 進行加熱，約 90 分鐘~兩個小時分解完畢，此時溶液呈現透明藍綠色。將溶液置於室溫下冷卻等待顏色透明
4. 使用凱氏氮測定機器約五分鐘後，使用處理過後錐形瓶內的溶液進行滴定(用 0.1N 的 NaOH)。※錐形瓶內的接收液內：25 mL 的 0.1 N 硫酸 + 2 滴甲基紅
5. 待瓶中顏色轉變成淡黃色滴定停止

粗蛋白(%) = 〔(空白組滴定量 mL - 樣品滴定量 mL) × 0.0014 × 1 × 6.25〕/ 樣品重(g) × 100%

Appendix 1.4. 中洗纖維(Neutral detergent fibers, NDF)分析法 (van Soest *et al*., 1991)：

I. 前置作業：

1. 將玻璃坩鍋(IWAKI; Code:32940FNL; SIZE:2G2; Q'TY:2)沖洗乾淨，並使用震盪機器震盪 30 分鐘(溫度設定在 20℃)
2. 使用酸性溶液酸洗(鹽酸:水=1:3)，overnight
3. 將玻璃坩鍋取出，沖洗並使用灰化爐灰化至少 4 小時
4. 從灰化爐取出坩鍋冷卻後沖洗，放入 105℃烘箱烘乾備用

II. 分析步驟：

1. 先將玻璃坩鍋從烘箱內取出，並放入乾燥皿中冷卻秤重。**(空坩鍋重)**
2. 放入濾紙(Whatman; Cat No 1822-047 47mm)，並再次放入烘箱內烘乾
3. 兩小時後，取出後放入乾燥皿內等待冷卻並秤重
4. 秤取樣品粉末 0.5 g~1 g 於 1000 mL 燒杯中，加入 50 mL 的中洗溶液、0.5 g Na2SO3 (關東；37285-00)以及 2 mL Decalin (Riedel-de haën)，並將迴流冷卻水打開
5. 待溶液沸騰約 30 分鐘後，再加入 50 mL 的中洗溶液以及 100 μL 的 Heat stable-amylase (SIGMA; A3306)，再沸騰 30 分鐘
6. 以玻璃坩鍋抽氣過濾，將沸騰的溶液倒入坩鍋中，並抽氣過濾。並用 80℃熱水沖洗附著在燒杯上的剩餘物
7. 以熱水沖洗坩鍋內的樣本，並使用玻璃棒攪拌。沖洗至無泡沫且液體澄清。
8. 以 Acetone (博盛)清洗兩次(清洗至不褪色)
9. 放入 105℃的烘箱，至少烘乾 8 小時
10. 放入乾燥皿中冷卻後秤重。**(NDF + 坩鍋重)**
11. 移入灰化爐中，使用 600℃灰化至少六小時

12. 放入乾燥皿後冷卻秤重**(灰化 + 坩鍋重)**

NDF(%) = 〔(NDF + 坩鍋重) - 空坩鍋重〕-〔(灰化 + 坩鍋重) - 空坩鍋重〕/ 樣品重 × 100%

III. 中洗溶液配製：

藥品名稱	重量(g)	廠商
Sodium lauryl sulfate (SDS)	30.0	片山, S0627 (FW: 288.38)
Disodium Ethylenediaminetetraacetate, EDTA	18.6	Bioshop 慧眾科技 Lot No:3464B14
sodium borate decahydrate (sodium tetraborate) ($Na_2B_4O_7 \cdot 10H_2O$)	6.81	片山, S-0365 (FW:381.37)
Di-Sodium hydrogen phosphate dehydrate ($Na_2HPO_4 \cdot 2H_2O$) 或是使用 4.56g 的 Anhydrous Na_2HPO_4	5.72	Merck, 1.06580
2-ethoxyethanol (2(2 ethoxyethoxy) ethanol) ($C_6H_{14}O_3$)	10mL	ACROS, 111-90-0 (FW: 134.17)

混合後使用定量瓶加 dd 水定量至 1000 mL

Appendix 1.5. 酸洗纖維(Acid detergent fibers, ADF)分析法(Goering and van Soest, 1970)：

I. 前置作業：

1. 將玻璃坩鍋(IWAKI; Code:32940FNL; SIZE:2G2; Q'TY:2)先沖洗乾淨，並使用震盪機器震盪 30 分鐘(溫度設定在 20℃)
2. 使用酸性溶液酸洗(鹽酸:水=1:3)，overnight
3. 將玻璃坩鍋取出，沖洗並使用灰化爐灰化至少 4 小時
4. 從灰化爐取出坩鍋冷卻後沖洗，放入 105℃烘箱烘乾備用

II. 分析步驟：

1. 將樣本放入 105℃烘箱中，2 小時
2. 先將玻璃坩鍋從烘箱內取出，並放入乾燥皿中冷卻秤重。**(空坩鍋重)**
3. 放入濾紙(Whatman; Cat No 1822-047 47mm)，並再次放入烘箱內烘乾
4. 兩小時後，取出後一樣放入乾燥皿內等待冷卻並秤重
5. 秤取樣品粉末 0.5 g~2 g 於 1000 mL 燒杯中，加入 100 mL 的中洗溶液，並將迴流冷卻水打開
6. 待溶液沸騰加熱 60 分鐘
7. 以玻璃坩鍋抽氣過濾，將沸騰的溶液倒入坩鍋中，並抽氣過濾。並用 80 ℃熱水沖洗附著在燒杯上的剩餘物
8. 以熱水沖洗坩鍋內的樣本，並使用玻璃棒攪拌。沖洗至無泡沫且液體澄清
9. 以 Acetone (博盛)清洗兩次(清洗至不褪色)
10. 放入 105 ℃的烘箱，至少烘乾 8 小時(overnight)。**(分析完 ADL 後再灰化)**
11. 放入乾燥皿中冷卻後秤重。**(ADF ＋ 坩鍋重)**
12. 移入灰化爐中，使用 600℃灰化至少六小時

13. 放入乾燥皿後冷卻秤重**(灰化+坩鍋重)**

ADF(%)=〔(ADF + 坩鍋重) - 空坩鍋重〕-〔(灰化 + 坩鍋重)-空坩鍋重〕/樣品重 × 100%

III. 酸洗溶液配製：

藥品名稱	重量(g)	廠商
N-Cetyl-N, N, N-trimethylammonium bromide (cetyltrimethylammonium bromide)(CTAB) ($C_{19}H_{42}BrN$)	20	Merck, 1.02342 (FW364.46)
1 N H_2SO_4	30 mL 的 98% H_2SO_4 定量加水加至 1000 mL	Merck (1.00748.2500)

將 CTAB 加至 1N 的 H_2SO_4 定量至 1000 mL

Appendix 1.6. 酸洗木質素(Acid detergent lignin, ADL)分析法(AOAC, 1984)：

I. 前置作業：

先將含有 ADF 玻璃坩鍋從烘箱內取出，並放入乾燥皿中冷卻秤重。**(ADF + 坩鍋重)**

II. 分析步驟：

1. 取 ADF 分析過後的樣品，加入 72%的 H_2SO_4 (Merck; 1.00748.2500)
2. 使其浸泡在 72% H_2SO_4 中至少 4 小時
3. 以煮沸熱水沖洗至中性
4. 以 Acetone 清洗兩次(清洗至不褪色)
5. 放入 105℃的烘箱，至少烘乾 8 小時(overnight)
6. 放入乾燥皿中冷卻後秤重。**(ADL + 坩鍋重)**
7. 移入灰化爐中，使用 600℃灰化至少六小時。
8. 放入乾燥皿後冷卻秤重**(灰化 + 坩鍋重)**

ADL(%) = 〔(ADL + 坩鍋重) - (空坩鍋重)〕 -〔(灰化+坩鍋重) - 空坩鍋重〕/樣品重 × 100%

Appendix 1.7. 總酚(Total phenolics)測定方法(Velioglu *et al*., 1998)：

I. 葉片冷凍乾燥的製備

1. 取葉片放入研缽中，並同時加入液態氮磨碎，隨後將樣本放入塑膠瓶中
2. 將已磨碎裝好樣本的塑膠瓶放入冷凍乾燥機中，冷凍抽乾。(24 小時/-50℃)

II. 萃取

1. 秤取 0.05 g 的樣本放入 2 ml 離心管中，並先加入 1 ml 的 80%甲醇(methanol)(包含有 1%鹽酸)，放在水浴槽震盪上 30 分鐘
2. 使用離心機離心(12000 rpm)15 分鐘，取上清液放到新的 2 ml 離心管中，並且重複以上步驟一次
3. 將抽取的上清液到新的 2 ml 離心管(第二次抽取上清液應徹底抽完)，並保存在 4℃

III. 反應

1. 取上清液到新的離心管，並加水至 100 μL。接著在試管內加入 0.75 ml 的 FC 試劑(FC 試劑：DDW=1：9；3 ml 的 FC 試劑 + 27 ml 的 DDW)，並使用 pipette 充分混合
2. 置於 22℃下五分鐘
3. 加入 0.75 ml 過飽和碳酸氫鈉(Na_2CO_3)，充分混勻
4. 將溶液置於 22℃，1.5 小時，測量波長 725 nm 吸光值。(使用 RO 水當作 blank 校正)

IV. 標準品的測定

1. 取 0.02 g 的沒食子酸粉末(精秤 0.0200 g)加入 0.4 ml 乙醇(95%酒精)，之後取出

0.2 ml 加 DDW 1.8 ml。(此時濃度為 5 mg/ 1 L)

2. 分別取 0 μL、10 μL、20 μL、50 μL、70 μL、100 μL 加水至 1000 μL。
   (此時濃度分別為：0 mg/L、50 mg/L、100 mg/L、250 mg/L、350 mg/L、500 mg/L)
3. 各別吸取 100 μL 至新的 eppendorf 中，並加入 0.75 ml 10%的 FC 試劑，計時五分鐘
4. 加入 0.75 ml 過飽和 Na_2CO_3，等待 1.5 小時測量波長 725 nm 吸光值
5. 將不同濃度沒食子酸的吸光值繪製成表，求出 R^2，其值必須要大於 0.97。之後即可使用內插法求出樣本總酚的含量

Appendix 2. Tables

Appendix 2.1. The values of standardized palatability, 7 chemical compounds, toughness and abundance of plants in three seasons. The bottomlines of the table give the correlation and regression coefficients of the relationships between palatability and 7 chemical compounds, toughness and abundance.

ID	Palatability	Dry matter	CP	NDF	ADF	ADL	Ash	Total phenolics	Toughness	Abundance
MYN	0.7467	0.4844	0.1338	0.7686	0.4725	0.1190	0.1096	0.0133	86.40	0.2970
MAR	0.4921	0.2338	0.0900	0.3624	0.3129	0.0385	0.0997	0.0113	95.80	0.0000
MET	0.3677	0.1707	0.1638	0.3657	0.2274	0.0397	0.1328	0.0064	43.73	0.0103
MDT	0.2083	0.3408	0.0808	0.5866	0.4702	0.2171	0.0441	0.0481	161.50	0.0000
MDJ	0.1486	0.2421	0.0647	0.7810	0.5300	0.1023	0.0338	0.0137	135.03	0.1166
JYN	0.9745	0.3778	0.1567	0.7867	0.3730	0.0613	0.0899	0.0097	92.40	0.2806
JAR	0.4914	0.1817	0.1002	0.3453	0.3289	0.0452	0.0945	0.0103	93.03	0.0050
JET	0.5808	0.1210	0.1467	0.2923	0.2497	0.0286	0.1573	0.0088	49.63	0.0200
JDT	0.2050	0.2672	0.0981	0.5486	0.4916	0.2108	0.0518	0.0284	175.93	0.0430
JDJ	0.1342	0.5429	0.0571	0.7641	0.4619	0.0742	0.0345	0.0085	237.90	0.1710
NYN	0.7871	0.4200	0.1623	0.8179	0.3820	0.0763	0.1030	0.0169	101.73	0.2820
NAR	0.5356	0.2319	0.0947	0.3416	0.3149	0.0425	0.1031	0.0118	87.40	0.0046
NET	0.5750	0.1463	0.1393	0.3344	0.2257	0.0373	0.1610	0.0090	51.30	0.0106
NDT	0.2530	0.3422	0.1182	0.5449	0.3959	0.1785	0.0546	0.0306	203.27	0.0070
NDJ	0.2676	0.2863	0.0798	0.8148	0.4400	0.0777	0.0377	0.0070	341.80	0.2013

Correlation and regression analysis										
	Palatability	Dry matter	CP	NDF	ADF	ADL	Ash	Total phenolics	Toughness	Abundance
MIN	0.1342	0.1210	0.0571	0.2923	0.2257	0.0287	0.0338	0.0064	43.7333	0.0000
MAX	0.9745	0.5429	0.1638	0.8179	0.5300	0.2171	0.1610	0.0481	341.8000	0.2970
P Value		0.8499	**0.0016**	0.9761	0.1316	0.0872	**0.0109**	0.1935	**0.0229**	0.0793
r Value		0.0535	0.7407	0.0085	-0.4076	-0.4565	0.6356	-0.3555	-0.5818	0.4669
R square		0.0029	0.5487	0.0001	0.1661	0.2084	0.4040	0.1263	0.3385	0.2181

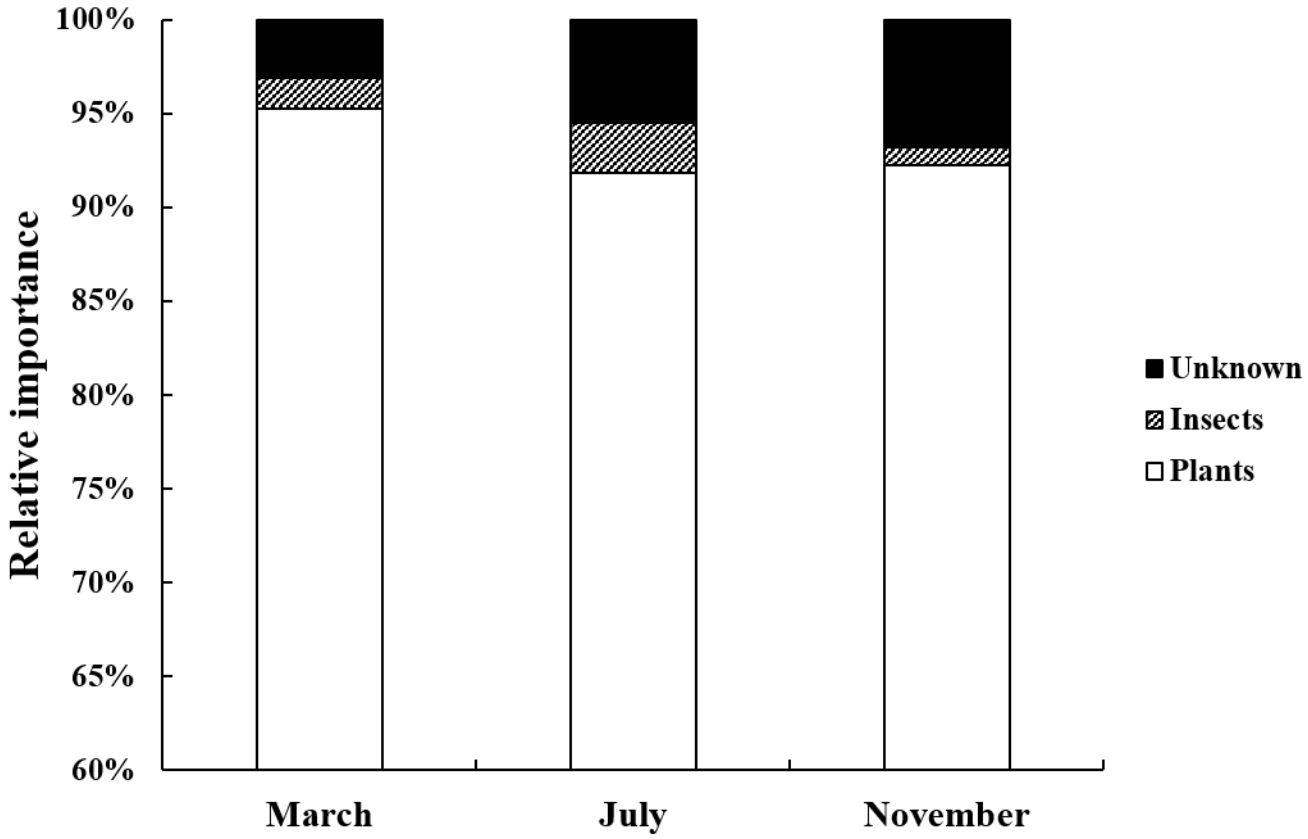
Note: Abbreviation for: M - March; J - July, N - November; YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, DJ - *Dicranum japonicum* 日本曲尾苔.

Appendix 2.2. The relationship between standardized palatability and 7 chemical compounds based on a stepwise multiple regression, N = 15.

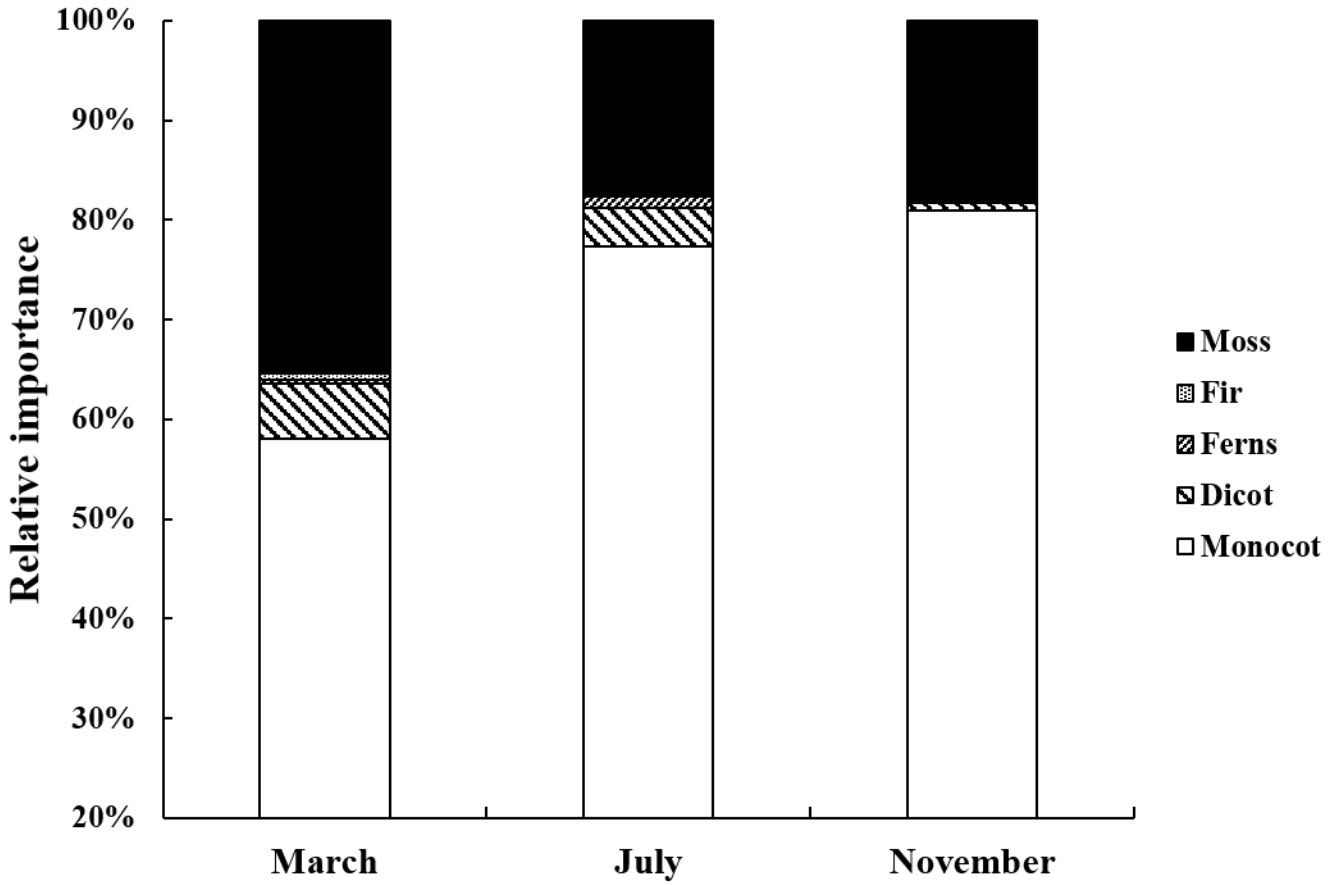
Variables	Parameter Estimate		Regression Model	
	β	R^2	$F_{1, 13}$	p
Intercept	-0.14		0.8	0.39
Crude Protein	5.25	0.55	15.8	**0.002**

Appendix 3. Figures

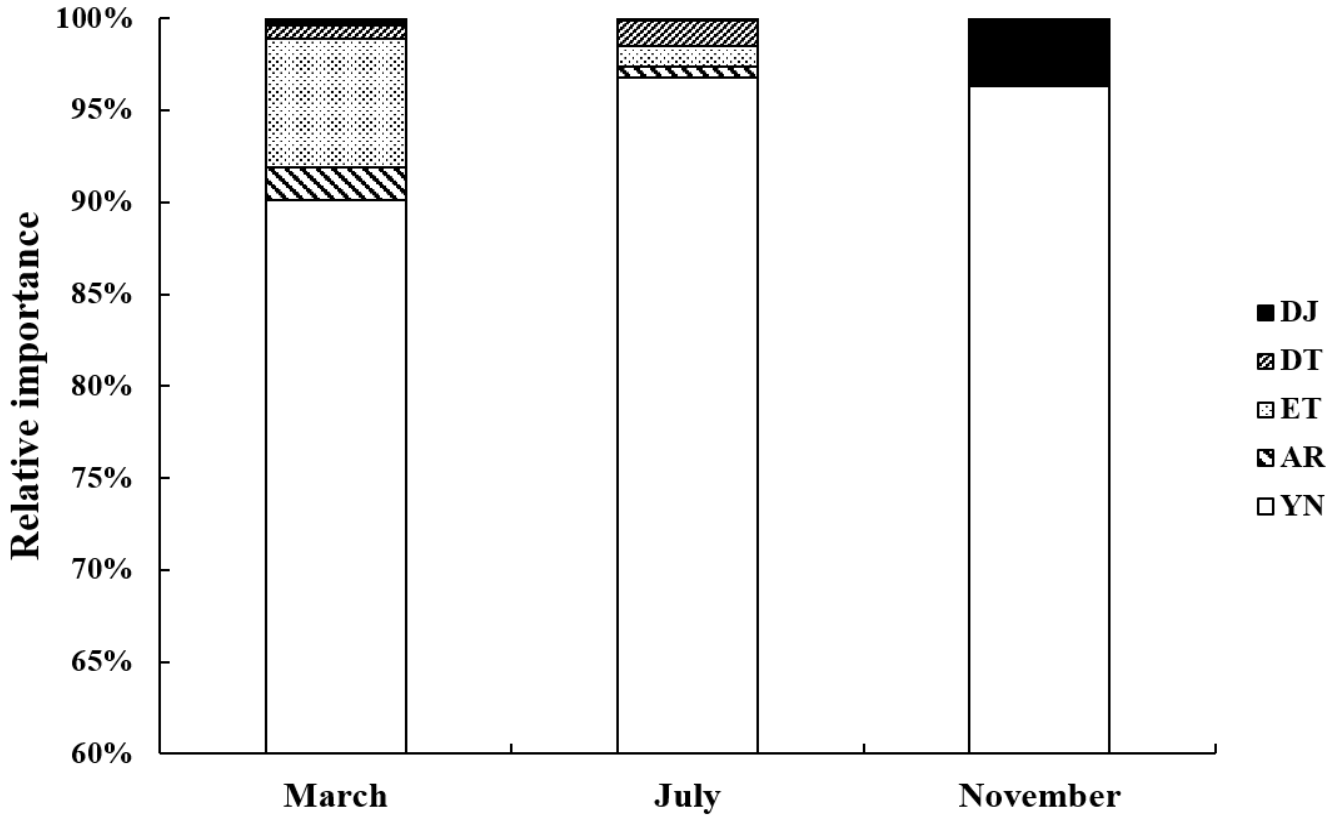
Appendix 3.1. Arrangement in a feeding trial, including tested plant materials, sweet potato, oats and newspapers as bedding.



Appendix 3.2. Relative importance of main food items (Plants, insects and unknown) in three seasons (n = 10 in each season).



Appendix 3.3. Relative importance of plants (divided into: Monocots, doicots, ferns, fir and moss) in three season (n = 10 in each season).



Appendix 3.4. Relative importance of plants in diets that were also used in feeding trials (including YN - *Yushania niitakayamensis* 玉山箭竹, AR - *Ainsliaea reflexa* 玉山鬼督郵, ET - *Elatostema trilobulatum* 裂葉樓梯草, DT - *Dryopsis transmorrisonensis* 玉山擬鱗毛蕨, and DJ - *Dicranum japonicum* 日本曲尾苔) in three season (n = 10 in each season).