

Dietary Overlap Among Axis, Fallow, and Black-tailed Deer and Cattle

HENRY W. ELLIOTT III AND REGINALD H. BARRETT

Abstract

Seasonal diets of native Columbian black-tailed deer (*Odocoileus hemionus columbianus*) and exotic axis deer (*Axis axis axis*), fallow deer (*Dama dama dama*), and cattle (*Bos taurus*) on Point Reyes National Seashore were determined by microhistological technique to assess their dietary overlap. Throughout the year black-tailed deer ate mostly forbs, axis deer and fallow deer ate mostly grasses and forbs, and cattle ate mostly grasses. Only a few plant species comprised most of their diets. Percent composition of food species was not related to their preference indexes. Diets of axis and fallow deer overlapped more with each other and cattle than with black-tailed deer except during the summer when the dietary overlap among all species was similar at a lower level. Comparison of seasonal diets of deer with this and other studies indicated that food consumption of deer was not limited to particular food classes.

Authors are former graduate student, Department of Agronomy and Range Science, University of California, Davis and now consulting biologist, 1012 Sand Bar Circle, Carmichael, Calif. 95608; and associate professor, Department of Forestry and Resource Management, University of California, Berkeley.

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Exotic ungulates introduced into favorable habitats may erupt in numbers, deplete their food resources, and then crash (Scheffer 1951, Klein 1968, Caughley 1970). At Point Reyes National Seashore, as a result of an introduction of 2 species of exotic deer during the 1940's and early 1950's (Wehausen and Elliott 1982) and the continuation of commercial beef and dairy operations, 4 ungulates now coexist in the Seashore's pastoral zone: cattle (*Bos taurus*); Indian axis deer (*Axis axis axis*), European fallow deer (*Dama dama dama*); and native Columbian black-tailed deer (*Odocoileus hemionus columbianus*).

Previous studies at Point Reyes National Seashore (Elliott 1973, Wehausen 1973) suggested that these deer and cattle have similar diets, and that unlimited growth of the exotic deer population could have significant negative effects on the nutrition of all resident ungulates, particularly in the fall when the amount of the forage and its nutritional value are low. Since the National Park Service was shooting the exotic deer within the pastoral zone to maintain their density at 1973 levels and knowledge of the ecological relationships between these species and their habitat was limited, this project was undertaken to provide information on which to base management decisions.

Many studies have indicated that competitive effects between sympatric ungulate species involved the use of food (Anthony and Smith 1977, Sinclair 1977, Mackie 1978, McCullough 1980, Kasworm et al. 1984). Therefore, to investigate the likelihood of competition among deer and between deer and cattle at their current densities on Point Reyes Peninsula, the botanical composition of their diets, their preference for these food species, and their dietary overlaps were assessed.

The Study Area

Point Reyes National Seashore includes 259 km² (100 mi²) of Point Reyes Peninsula in Marin County, California, 32 km (20 mi) northwest of San Francisco. Ranch lands of 81 km² (31 mi²) comprise the pastoral zone of the Seashore.

Black-tailed deer are present throughout the study area. Axis and fallow deer range east and northeast of Drakes Estero (Wehausen and Elliott 1982).

Climax vegetation near the coast is a mosaic of northern coastal scrub and coastal prairie (Elliott and Wehausen 1974). Bishop pine forest and northern coastal scrub are dominant farther inland (Grams et al. 1977). Much of the pastoral zone has been cleared and seeded to pasture species which are maintained by periodic burning, plowing, and reseeding.

Most of the rain falling on the study area occurs in winter with some rain in fall and spring. Summer moisture is derived from advection fog that condenses on plants and drips to the ground. The average annual rainfall at Point Reyes Lighthouse was 45.7 cm (18.0 in) in 1942 (U.S. Weather Bureau 1942). A total of 69.0 cm (29.9 in) of rain fell at the Murphy Ranch in the pastoral zone between 1 September 1979 and 31 August 1980. The total rainfall at the nearby Bear Valley ranger station was 24% less during 1978-79 than during 1979-80. Mean January temperature at the Lighthouse was 9.8°C (49.6°F); mean July temperature was 12.1°C (53.7°F) (U.S. Weather Bureau 1942).

Methods

Dietary Composition

During April 1979 thru March 1980 esophageal, rumen, and fecal samples were taken monthly from 6 steers (3 Hereford and 3 Hereford-Angus crosses) which had both esophageal and rumen fistulas (Van Dyne and Torell 1964, Holechek et al. 1982). On a sampling day the steers were gathered at dawn, fitted with esophageal collection bags that had screened bottoms to remove saliva, and released together to graze for 1 hour. Samples were taken from the esophagus, rumen, and colon (feces) on 5 days each month within 10 days and preserved in stock formalin. Equal amounts of the 30 samples from each of the esophagus, rumen, and colon were pooled by month. The steers grazed on a 5.6-ha (14-acre) pasture with a vegetal composition judged to be typical of the pastoral zone. A mixture of 20% sodium chloride, 20% monosodium phosphate, and 60% sodium bicarbonate was available on demand to compensate for electrolytes lost from saliva dripping from around the esophageal cannula. Availability of forage species was sampled monthly with a step-point transect of approximately 300 points across the pasture (Evans and Love 1957).

Dietary samples of axis and fallow deer were taken from rumens of deer shot during 7 months from October 1977 through September 1978. Black-tailed deer dietary samples were collected from rumens of deer shot in 12-different months between May 1977 and October 1980. All rumen samples were oven dried at 60°C (140°F), ground thru a Wiley mill with a screen of 1-mm mesh, and pooled by month with a minimum of 5 subsamples of equal volume from different deer.

The dietary samples were analyzed for relative plant species density using a microhistological method (Sparks and Malechek 1968). A sample was ground through a 1-mm screen, bleached, stained with hematoxylin and safranin, and mounted on microscope slides with a gum arabic-Karo syrup medium (Truman et al. 1983).

Twenty fixed locations on each slide were viewed thru a compound microscope at 100 power. In each of the 100 fields the occurrences of identifiable plant species were noted. The frequency of each species was converted into relative density as an estimate of the percent composition by dry weight. Species names followed Howell (1970).

If consistent differences in food species or classes between collection sites at the esophagus, rumen, and colon had occurred, then the relative composition of deer rumen samples could have been corrected to that of the esophageal samples (Dearden et al. 1975). However, linear regression analysis of esophageal, rumen, and fecal samples on each other by food classes (grass, forb, browse) found in the steer diet during 12 months had very low coefficients of determination (Table 1). Botanical composition of rumen and

Table 1. Linear regression of steer food classes by pooled esophageal, rumen, and fecal samples collected monthly (N=12).

Food class	b	a	r ² × 100	SD
Grass:				
Esophageal on rumen	-0.20	93.0	2.7	11.8
Esophageal on fecal	-0.08	85.0	1.0	11.9
Rumen on fecal	0.40	47.6	33.1	8.1
Forb:				
Esophageal on rumen	0.36	10.8	3.9	8.7
Esophageal on fecal	0.37	10.3	7.1	8.5
Rumen on fecal	0.35	8.6	20.5	4.4
Browse:				
Esophageal on rumen	-0.08	4.4	2.4	5.1
Esophageal on fecal	-0.01	5.1	6.1	5.0
Rumen on fecal	0.61	0.9	67.3	5.4

b = regression coefficient, a = Y intercept, r² = coefficient of determination, SD = standard deviation of the estimate about the regression line.

corresponding fecal samples of 4 black-tailed deer collected in September 1978 were also analyzed for differences in composition between collection sites. Only 50% of the 12 plant species analyzed had linear regression equations with coefficients of determination greater than 75% (Table 2). Therefore, unweighted, percent composition of plant species from rumen samples were used as the best approximation of deer diets. Unweighted values from esophageal samples were used to represent cattle diets.

Table 2. Linear regression of dietary composition of black-tailed deer by food class and by food species of rumen on fecal collection sites. Four deer were sampled in September 1978.

Species	b	a	r ² × 100	SD
Grass:				
<i>Danthonia californica</i>	0.1	0.2	22.5	0.4
<i>Festuca dertonensis</i>	0.5	0.1	31.7	0.2
<i>Holcus lanatus</i>	0.2	0.1	4.8	0.5
Forb:	3.0	-190.0	74.2	16.4
<i>Achillea borealis</i>	0.1	0.7	2.6	1.8
<i>Hypochaeris radicata</i>	0.0	1.1	88.7	0.2
<i>Plantago lanceolata</i>	1.3	13.3	77.7	13.6
Browse:	2.2	6.7	41.8	20.2
<i>Corylus californica</i>	0.0	0.0	100.0	0.0
<i>Lonicera hispidula</i>	0.2	0.0	27.4	5.8
<i>Myrica californica</i>	0.4	-0.1	99.6	0.1
<i>Rhamnus californica</i>	0.7	0.3	80.8	0.8
<i>Rubus ursinus</i>	9.2	6.5	89.7	11.3
<i>Vaccinium ovatum</i>	0.0	0.1	11.1	0.2

b = regression coefficient, a = Y intercept, r² = coefficient of determination, SD = standard deviation of the estimate about the regression line.

Dietary Overlap

A dietary overlap index recommended by Abrams (1980) to assess the relative amount of food species eaten in common by each pair of ungulate species was calculated as follows $\sum_{i=1}^n (\min A_i, B_i)$ where A_i and B_i are the percentages of plant species i eaten by ungulates A and B and n is the total number of plant species in both ungulate diets.

Dietary Preference

The preference of a food species for deer and cattle was calculated by subtracting the proportion of the species available in the environment from the proportion of the species in the diet (Strauss 1979). This index has values that range from 1 to -1. Species with values greater than 0 are preferred. Species with values less than 0 are avoided. Species with values near 0 are consumed without regard to choice. Preference indexes were calculated from steers for 12 months using estimates of dietary composition and monthly, step-point samples. Preference indexes were calculated for deer for 3 months (January, May, and September) using estimates of their dietary composition and the average of the estimates of botanical cover on 3 sites in the pastoral zone (Elliott 1983). Only species comprising over 2% of the diet or the environment were considered.

Results

Dietary Composition and Preference

Comparisons of the monthly diets of the 4 ungulates by food class (Fig. 1) show that: (1) The diets of axis and fallow deer

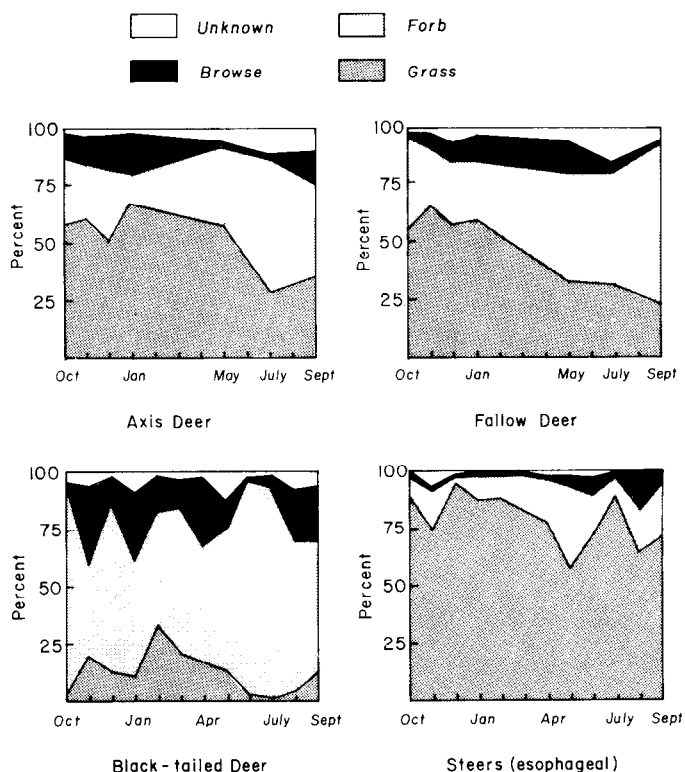


Fig. 1. Percent composition of the monthly diet of black-tailed deer, axis deer, fallow deer, and cattle on Point Reyes Peninsula. Deer and steer diets are based on analysis of pooled rumen and esophageal samples, respectively.

consisted of more grass in the fall, winter, and spring than in the summer when they ate more forbs than grass. However, their annual diet consisted of more grass than did that of black-tailed deer. (2) Black-tailed deer ate a majority of forbs throughout the year and they ate more forbs and browse than did the exotic deer or

steers. (3) Steers ate a majority of grass throughout the year and a higher percentage of grass than did native or exotic deer.

A review of the diets of these 4 ungulates reveals that only a few plant species comprised the bulk of the diets (Elliott 1983). These plant species did not always have positive preference indexes because they were also abundant in the environment.

Agrostis spp. were heavily used grasses by exotic deer in the winter and spring but they had a preference index near 0.

Bromus spp., introduced annual and biennial grasses, were used by steers and exotic deer throughout the year and by black-tailed deer in February and March. They comprised over 50% of the steer diet from December through February. They were preferred by steers, axis deer, and fallow deer during the winter growing season.

Festuca dertonensis Aschers. & Graebn., an introduced annual grass, comprised about 10% of the diet of the 4 ungulates throughout most of the year. However, it had a near 0 preference index in January and a negative preference index in May and September.

Danthonia californica Boland., a native perennial grass, comprised more than 18% of the steer diet from August through November and was preferred in September when most of the other grasses and forbs had died. The exotic deer consumed significant amounts of *D. californica* throughout the year and preferred it in January.

Holcus lanatus L., an introduced perennial grass, was used by steers primarily during the summer months when the annual grasses and forbs had died.

Lolium perenne L., an introduced perennial, was the staple grass in the steer diet. Its greatest use by steers occurred from March through September when it was most abundant. The exotic deer consumed *L. perenne* during the fall when they gleaned its green basal leaves.

Erodium spp. and *Geranium dissectum* L. were important, introduced, annual forbs in the black-tailed deer diet during the winter and spring and had near 0 preference indexes except for a positive preference index for *G. dissectum* in May.

Hypochoeris radicata L., an introduced, prostrate, perennial forb, was consumed by black-tailed deer in moderate amounts nearly every month and had a positive preference index in January and May.

Lotus corniculatus L., an introduced perennial legume, was eaten by fallow deer during all months and comprised as much as 24% of the diet in the dry month of September when it was highly preferred.

Plantago lanceolata L., an introduced perennial, was the staple forb in the monthly diet of all 4 ungulate species. It was abundant in the environment and was highly preferred by black-tailed deer during January and September.

Trifolium spp., introduced and native annual forbs, were in the steer diet from November through January and April through June.

Ranunculus californicus Benth., a native annual forb, was important in the black-tailed deer diet during February and March.

Rumex acetosella L., an introduced annual forb, was prominent in the exotic deer diets during most of the 7 months sampled.

Pteridium aquilinum var. *pubescens* Underw. and *Polystichum munitum* Presl. are native ferns that were consumed by black-tailed deer in November and December.

Rubus ursinus C. & S., a native vine, was the most prominent browse in the diet of black-tailed deer. Steers consumed some *R. ursinus* during the summer months.

Salix spp., native willows, were heavily used during November, and were used slightly in most other months by black-tailed deer.

Dietary Overlap

The monthly, dietary, overlap indexes for the 6 possible comparisons among the 4 ungulates (Fig. 2) show that: (1) Axis and fallow deer had the greatest and most constant dietary overlap throughout the year. (2) Black-tailed deer diets overlapped with axis deer as

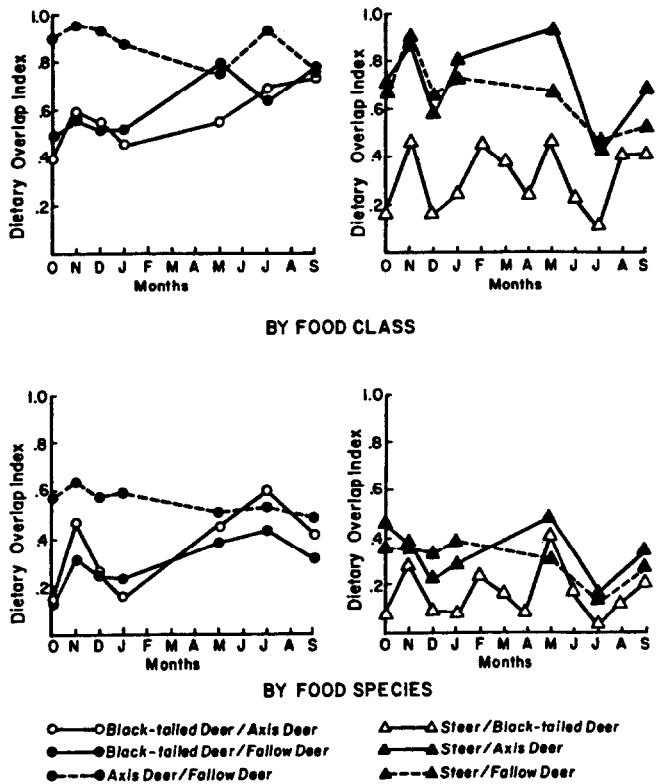


Fig. 2. Dietary overlap between the 6 possible paired comparisons of black-tailed deer, axis deer, fallow deer, and steers by food class (grass, forb, browse) and by food species on Point Reyes Peninsula.

much as with fallow deer. The overlap was highest in the summer and lowest in the fall and winter. (3) Black-tailed deer and steers had the lowest dietary overlap. (4) The overlaps of the steer diet with the diets of both axis and fallow deer were similar throughout the year.

Discussion

Estimation of the botanical composition of the deer diet from partially digested rumen samples is difficult. Plant species have different amounts of indigestible lignin which form the identifiable features of their cuticles. Consequently, after digestion in the rumen some plant species will register a higher composition than before digestion (Vavra et al. 1978, Gaare et al. 1977, McInnis et al. 1983). Because the percent composition of a species is dependent on the amount of all other species in the sample, differential digestibility of food species causes the percent composition of rumen and fecal samples to vary depending on the species eaten. Steer diets determined from esophageal, rumen, and fecal samples were different (Fig. 3). However, diet comparisons by food classes resulted in a greater similarity between sites of sample collection because fewer categories were being compared. Also, Dearden et al. (1975) found that the inaccuracies inherent in the microhistological technique did not alter the relative importance of species in rumen samples from the relative importance of species known to be in the actual diet.

Seasonal food habits by food class (grass, forb, browse) from many studies of ungulates were plotted on triangular-coordinate grids by Van Dyne et al. (1980). We have used their technique and data for black-tailed deer taken from studies in Mendocino County, California (Longhurst et al. 1979) and added data for seasonal food classes of black-tailed, axis, and fallow deer and cattle from Point Reyes Peninsula and axis and fallow deer elsewhere (Fig. 4). Van Dyne et al. (1980:299) explain: "To read these triangle-coordinate graphs you should realize that the magnitude of the variable (food class) increases the further you go away from

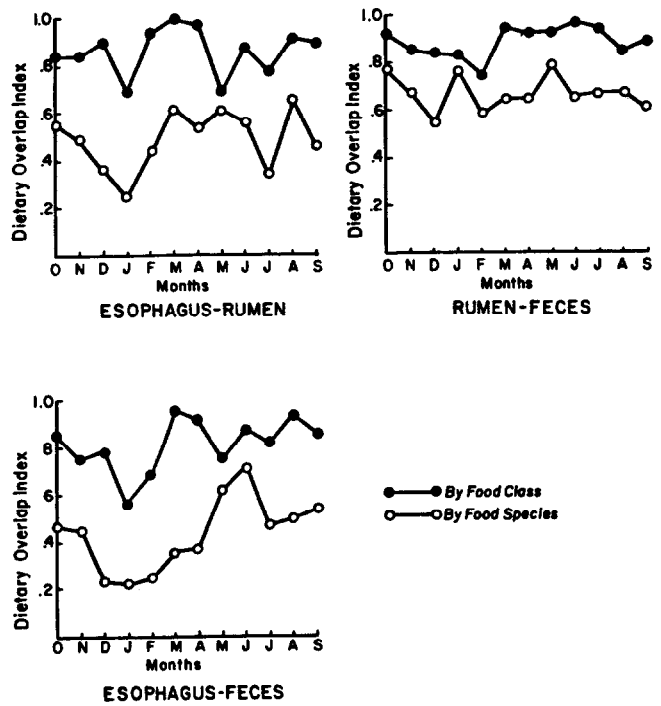


Fig. 3. Similarity of the estimates of the steer diet on Point Reyes Peninsula derived from esophageal, rumen, and fecal samples using the dietary overlap index. The diets are compared by food class (grass, forb, browse) and by food species.

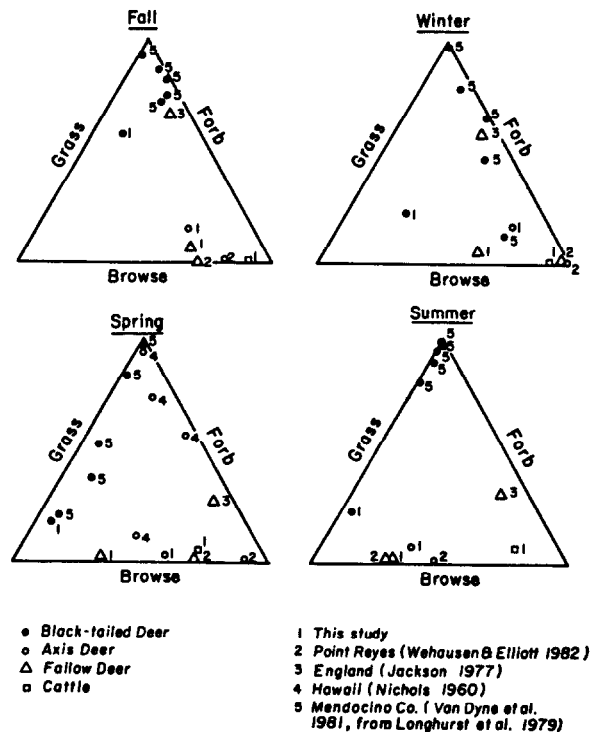


Fig. 4. Diet by food class of black-tailed deer, axis deer, fallow deer, and cattle at the indicated locations. See text for method of interpreting the triangular-coordinate plots.

the axis on which the name occurs. Each component ranges from 0 to 100%. A point on any margin means that value is 0% for the component labelled on the side of the graph."

The spread of points for the 3 deer species on the triangular-

Table 3. Percentage of native and exotic plant species on summer pastures and consumed by native and exotic ungulates as calculated from averages of monthly esophageal values for steers and rumen values for deer (Elliott 1983).

Origin	Summer Pastures	Black-tailed Deer ¹	Steer ²	Axis Deer ²	Fallow Deer ²
Native	13.5	41.5	14.9	26.1	22.9
Exotic	82.6	53.1	74.8	51.5	61.4
Unknown	3.9	5.3	10.2	22.4	15.7

¹Native species.

²Exotic species.

coordinate plots (Fig. 4) implies that no single species specialized on a particular class of forage. Each deer species ate what was available and palatable. The varied diets of black-tailed deer, other than on Point Reyes Peninsula, were all from different vegetal types within the same general area. The axis deer in Hawaii were from low and high elevations on 2 different islands. These data were yearly averages that were placed in the spring triangle because of the availability of green vegetation. The English fallow deer data came from an area where forests are interspersed with open meadows.

Although food habits at different locations varied greatly, axis and fallow deer tended to eat more grass and less browse than black-tailed deer (Fig. 4). Both axis and fallow deer have spatulate, first incisors in contrast to the more narrow, first incisors of black-tailed deer. The wide, cutting edge of the axis and fallow deer first incisors, similar to the incisors of cattle, may be an adaptation to grazing. A study of axis deer food habits in the scrub oak habitat of Texas (not included in the triangular coordinate plots because the data had been pooled for 2 different vegetal types) found that grass comprised the majority of the axis deer diet at all seasons except for fall of a year when acorns were abundant and readily eaten (Smith 1977).

An extensive survey of the seasonal food habits of cattle by Van Dyne et al. (1980) found a trend not much different from the seasonal diets of steers at Point Reyes. Cattle on Point Reyes Peninsula and elsewhere tended to eat more grass and less forbs and browse at all seasons than axis, fallow, and black-tailed deer.

Anatomical differences between cattle and deer have been used to explain their differences in food habits. Cattle have a larger body size, ratio of ruminoreticular volume to metabolic body weight, and mouth size than deer. This permits cattle to still consume large quantities of grasses during seasons when grasses have low nutritional value, while deer tend to choose selectively less abundant forbs and browse parts which have higher nutritional value (Hanley and Hanley 1982).

Secondary compounds in plants that have evolved to deter herbivory would also be expected to affect dietary composition (Longhurst et al. 1968, Freeland and Janzen 1974, Nagy and Regelin 1975). However, native food species were more prominent in the native black-tailed deer diet than in either the exotic deer or cattle diets on Point Reyes Peninsula, even though exotic plant species in the grassland during the summer had a much higher percent composition than native plant species (Table 3).

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