

Effects of spines and thorns on Australian arid zone herbivores of different body masses

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Summary. We investigated the effects of thorns and spines on the feeding of 5 herbivore species in arid Australia. The herbivores were the rabbit (*Oryctolagus cuniculus*), euro kangaroo (*Macropus robustus*), red kangaroo (*Macropus rufus*), sheep (*Ovis aries*), and cattle (*Bos taurus*). Five woody plants without spines or thorns and 6 woody plants with thorns were included in the study. The spines and thorns were not found to affect the herbivores' rates of feeding (items ingested/min), but they did reduce the herbivores' rates of biomass ingestion (g-dry/item). The reduction in biomass ingested occurred in two ways: at a given diameter, twigs with spines and thorns had less mass than undefended plants, and the herbivores consumed twigs with smaller diameters on plants with spines and thorns. The relative importance of the two ways that twigs with spines and thorns provided less biomass varied with herbivore body mass. Reduced twig mass was more important for small herbivores, while large herbivores selected smaller diameters. The effectiveness of spines and thorns as anti-herbivore defenses did not vary with the evolutionary history of the herbivores (i.e. native vs. introduced). Spines and thorns mainly affected the herbivores' selection of maximum twig sizes (reducing diameter and mass), but the minimum twig sizes selected were also reduced.

Key words: Herbivory – Australia, kangaroos – Plant-animal interactions – Plant defenses

Perhaps no other plant characteristic has so frequently been defined as a defense against herbivory as thorns and spines. However, the effectiveness of these structures in retarding herbivory is not always clear. In some in-

stances, these plant structures have a demonstrated effect and, in other cases, they do not (Cooper and Owen-Smith 1986; Lindroth 1989; Myers and Bazely).

In addition, our understanding of how thorns and spines retard herbivory is complicated by the different ways they can affect herbivores. First, thorns and spines can slow down the herbivore's ability to harvest food items (e.g. items ingested/min) by forcing it to be more careful when taking bites. This might occur when the herbivore attempts to avoid the potentially painful effect of the thorn or spine on its mouth. Second, the herbivore may bite off smaller portions of plants with spines or thorns (e.g. item size: diameter of branch consumed). This might be necessary so food items can be easily manipulated in the mouth to avoid the painful effects. Third, many plants with spines or thorns have reduced leaf size and number of leaves per item (e.g. dry mass of leaves per branch of a given diameter) (Myers and Bazely in press), so thorned or spined plants may provide less mass to the herbivore.

The above 3 factors can have an important influence on herbivore food selection. Herbivores select food items that provide at least a minimum intake of mass per unit of time (Belovsky 1981, 1984a, b, 1986; Cooper and Owen-Smith 1986), given the items are of sufficient nutritional quality to the herbivore. All three of the above factors tend to reduce the rate at which mass is ingested. This can reduce the acceptability of a plant with thorns or spines for the herbivore, if some items do not provide for the minimum rate of mass intake.

We investigated the effects of spines and thorns on food item selection by mammalian herbivores at an arid site in Australia. The herbivore species studied varied in body mass (2 to 400 kg) including native and introduced species. Using these data, we were able to compare statistically the relative effects of the three possible ways that spines and thorns might affect herbivores. Furthermore, we were able to address how the above three effects of spines and thorns might vary in importance to herbivores of different body masses and evolutionary history (native vs. introduced).

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Study site

The study was conducted at the University of New South Wales' Fowlers Gap Arid Zone Research Station which is located in northwestern New South Wales, Australia, approximately 112 km north of the town of Broken Hill (latitude 31° S, longitude 142° E). Two major types of habitats are present at the site: plains and low rocky ridges. The rocky ridges are dominated by an open canopy of mulga (*Acacia aneura*) and a wide variety of shrubs. The plains contain more grasses and forbs with a lesser variety of shrubs. Bare ground in both habitats is always greater than 70% of the area. The vegetation and abiotic environment have been described more fully elsewhere (Dawson et al. 1975; Croft 1981a, b).

All measurements were made in the early summer months of November and December, 1988. Woody plants in these environments comprise a large fraction of the standing crop biomass (65.4% on the rocky ridges and 41.4% on the plains) which makes them important food sources for the herbivores, especially as the summer progresses, and grasses and forbs become less abundant. Many of the woody plant species in this environment have thorns or spines, and these plants can comprise a large proportion of the woody plants (up to 50% of the woody biomass). At this time, the woody plants were no longer accumulating much new growth, so the thorns and spines were hardened.

Herbivore feeding observations were made on eleven common species of woody plants. Five of the woody plants did not possess spines or thorns. These were pop saltbush (*Atriplex holocarpa*), perennial saltbush (*A. vesicaria*), fan saltbush (*A. angulata*), satiny bluebush (*Maireana georgei*), and *Acacia burkitti*. Six woody plant species had spines or thorns. These were short-winged copperburr (*Sclerolaena brachyptera*), pale poverty bush (*S. divaricata*), gray copperburr (*S. diacantha*), cottonbush (*M. aphylla*), thorny saltbush (*Rhagodia spinescens*) and prickly wattle (*Acacia victoriae*). All of these plants are members of the family Chenopodiaceae, except for the two acacia species which belong to the family Mimosaceae.

Five species of mammalian herbivores were studied: european rabbit (*Oryctolagus cuniculus*: 1.5 kg, introduced); euro kangaroo (*Macropus robustus*: 32.5 kg, native); red kangaroo (*Macropus rufus*: 44.5 kg, native); domestic sheep (*Ovis aries*: 60 kg, introduced); and domestic cattle (*Bos taurus*: 400 kg, introduced). These herbivores depend heavily upon woody plants for food at this time of the year, since the amount of woody plants in their diets ranges from 14% (euro kangaroo females) to 75% (cattle) (unpubl. data).

Methods

Several plant measures were made:

1) A minimum of 15 twigs from each plant species was clipped over diameters ranging from approximately 0.01–10 mm during herbivore observations (see below). This range of twig sizes spanned those known to be fed upon by the herbivores, and provided ample

resolution of diameter-mass relationships for each plant species within the restricted range of diameters sampled (see RESULTS). Each twig was dried for 48 hr at 100° C and then the twig and leaf portions were weighed separately.

2) Lengths were measured for a sample of 20 spines or thorns from each plant species and the spines or thorns were identified as being straight vs. curved, and thorn acuity (sharpness) was categorized as dull vs. pointed.

3) Three samples composed of twigs from 5 different plants were collected for each woody species and chemically digested in HCl and pepsin (Terry and Tilley 1964). The samples were dried for 48 hr at 100° C and ground in a Wiley Mill with a 40 mesh screen. This chemical digestion method provides an index that is correlated with herbivore in vivo digestibility (Belovsky 1986) and with plant nitrogen content (A. Joern, pers. comm.). Furthermore, this method was chosen over other methods because it could be conducted on small quantities of plant material and large numbers of samples could be analyzed efficiently at low financial cost. This was an important consideration since, as part of our overall study, more than 1000 samples were analyzed.

Observations of the five herbivore species were made on free-roaming individuals. All observations were made from a vehicle (acting as a blind) to minimize disturbance of their foraging. Individual herbivores exhibited no behavioral indications of being disturbed and frequently were observed for periods in excess of an hour. All observations were made at distances no greater than 20 m using 7×35 binoculars or a 15–60× spotting scope. The number of individual animals observed for each herbivore species cannot be ascertained, because they were unmarked and free-roaming; however, observations were made for each species on a minimum of 10 occasions, i.e. different locations and/or days.

Using a stopwatch, we measured the amount of time an herbivore required to take 10 consecutive bites of a particular plant species. A bite was defined as the tearing or snipping motion used to remove items (twigs) from the plant. During these observations of 10 consecutive bites, if a ruminant stopped to chew regurgitated items, these observations were excluded from the analysis. We also measured the number of items (twigs) removed in a single bite. This was measured only when the herbivore was within 5 m of the observer.

During the feeding observations, the plant fed upon and location of feeding on the plant were noted by the observer. After a number of measurements had been made on an individual herbivore, the observer would return to the specific plants that had been browsed. The observer would then locate the items (twigs) removed. These could be identified based upon the freshness of the woody stem remaining and/or the presence of the herbivore's saliva. The diameter of each removed item (twig) at the point of browsing (tip of remaining stub) was measured using calipers. An adjacent uneaten twig on the same plant was clipped at the matching diameter. This matching twig was dried for 48 hr at 100° C and weighed to estimate the consumed item's mass.

The data were analyzed using ANOVA, ANCOVA and regression methods to assess the effects of thorns and spines on herbivore foraging behavior and plant selection. Proportions were arcsine transformed for statistical analysis, and significance was assessed at a probability level of 0.05. All statistics were conducted on a PC using the program SYSTAT (Wilkinson 1990).

Results

Significant allometric relationships emerged for all of the 11 woody plant species within the twig diameter range of 0.01–10 mm (r^2 varied with species from 0.29 to 0.96 with a mean of 0.65). However, the main determinants of the allometric relationship were not species specific (see below).

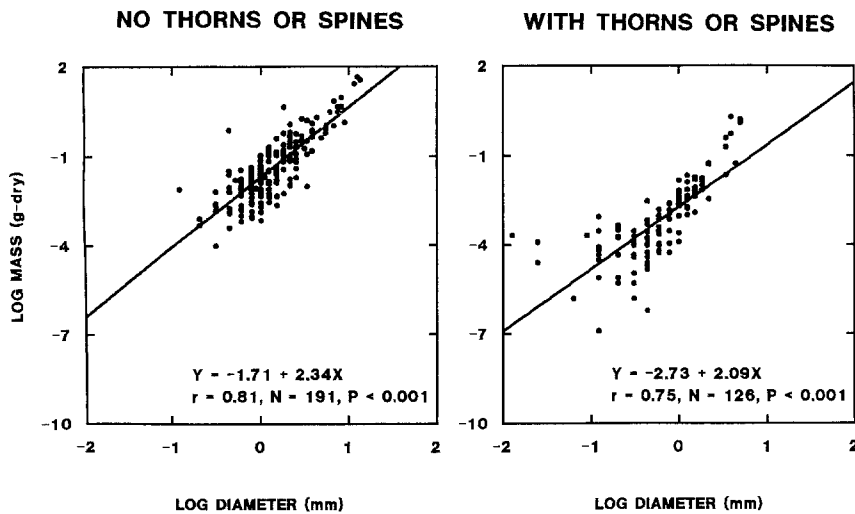


Fig. 1. The relationship between log twig diameter and log twig mass is presented for twigs from thorned and unthorned plants. The results of the regression analysis (line) are also provided

Table 1. Characteristics of the plants studied

Plant	Thorn			% Solubility in HCl & Pepsin
	Length (mm)	Shape	% Leaf mass	
Thorny saltbush <i>Rhagodia spinescens</i>	26.9 ± 12	Straight	45.2 ± 9	
Cottonbush <i>Maireana aphylla</i>	17.4 ± 6.7	Straight	22.5 ± 4.7	37.3 ± 1.1
Prickly wattle <i>Acacia victoriae</i>	11.8 ± 2.3	Curved	57.7 ± 11	33.7 ± 4.7
Gray copperburr <i>Sclerolaena diacantha</i>	8.7 ± 2.1	Straight	26.6 ± 16	36.6 ± 2.6
Short-winged copperburr <i>Sclerolaena brachyptera</i>	4.9 ± 0.9	Straight	36.8 ± 21	32.1 ± 2.5
Pale poverty bush <i>Sclerolaena divaricata</i>	0.5	Straight	57.3 ± 15	44.3 ± 3.5
Pop saltbush <i>Atriplex holocarpa</i>	0		79 ± 8.7	62.2 ± 0.6
Perennial saltbush <i>Atriplex vesicaria</i>	0		69.5 ± 9.6	52.6 ± 4
Fan saltbush <i>Atriplex angulata</i>	0		79.1 ± 6.8	62.5 ± 1.6
Satiny bluebush <i>Maireana georgei</i>	0		67 ± 4.2	37.7 ± 2.6
Acacia burkitti	0		65.8 ± 7.2	

An allometric relationship between twig diameter and twig mass for the pooled data was found (Fig. 1). There was no significant difference in the slopes for thorned and unthorned plants, or between species. Table 1 presents thorn and leaf mass characteristics for the different plant species. An ANCOVA comparing 1) log twig diameter, 2) presence/absence of thorns, and 3) thorn length with

log twig mass is presented in Table 2. All three independent variables are significant. Consequently, twig mass increased with diameter in the same way for thorned and unthorned plants, but thorned twigs had a lower mass at a given twig diameter than did twigs from unthorned species. Finally, twigs with long thorns had a lower mass at a given diameter. The above variables explain 76% of the variance in twig mass. Inclusion of plant species, as an additional category, accounted for only an additional 2% of the variance in an ANCOVA.

The proportion of twig mass that is made up of leaves also varies with the presence and absence of thorns (Table 1). Woody plants with thorns have proportionally less leaf mass at a given twig diameter than plants without thorns (ANOVA using arcsine transform of leaf proportion: $F = 99.43$; $DF = 1, 78$; $P \leq 0.0001$).

Table 2. The ANCOVA results relating plant characteristics to twig mass

Independent variable	DF	F	P
Log diameter	1,311	316.94	0.001
Presence/absence of thorns	1,311	38.8	0.001
Thorn length	1,311	3.65	0.05

Table 3. Harvesting characteristics for different herbivores eating thorned and unthorned plants are presented. Standard deviations and sample sizes are also given. The min/max values are the 10%

smallest and largest values, or the 3 smallest or largest values when 10% of the sample size is less than 3

Herbivore	Plant	Bite diameter (mm)			Bite mass (g-dry)			Bites/min
		min 10%	AVG.	max 10% (a)	min 10%	AVG.	max 10% (b)	
Rabbit	Thorns	0.40 ± 0.00 N=3	0.90 ± 0.37 N=19	1.55 ± 0.21 N=3	0.020 ± 0.003 N=3	0.06 ± 0.05 N=19	0.16 ± 0.04 N=3	20.00 ± 4.28 N=7
	No thorns	0.50 ± 0.10 N=3	0.95 ± 0.27 N=33	1.50 ± 0.27 N=3	0.040 ± 0.020 N=3	0.27 ± 0.36 N=33	1.24 ± 0.60 N=3	18.46 ± 10.05 N=23
Euro	Thorns	0.21 ± 0.06 N=4	0.64 ± 0.26 N=40	1.10 ± 0.08 N=4	0.004 ± 0.001 N=4	0.03 ± 0.04 N=40	0.13 ± 0.04 N=4	21.32 ± 8.70 N=5
	No thorns	0.73 ± 0.05 N=4	1.19 ± 0.28 N=36	1.63 ± 0.10 N=4	0.045 ± 0.013 N=4	0.25 ± 0.19 N=36	0.64 ± 0.10 N=4	21.60 ± 7.29 N=21
Red	Thorns	0.63 ± 0.06 N=3	0.84 ± 0.15 N=26	1.10 ± 0.10 N=3	0.016 ± 0.004 N=3	0.05 ± 0.03 N=26	0.12 ± 0.05 N=3	17.73 ± 5.68 N=6
	No thorns	0.58 ± 0.05 N=4	0.90 ± 0.23 N=39	1.36 ± 0.26 N=4	0.049 ± 0.009 N=4	0.16 ± 0.10 N=39	0.38 ± 0.07 N=4	17.52 ± 9.82 N=25
Sheep	Thorns	0.45 ± 0.07 N=3	0.95 ± 0.25 N=21	1.30 ± 0.00 N=3	0.002 ± 0.001 N=3	0.06 ± 0.05 N=21	0.16 ± 0.20 N=3	20.00 ± 4.28 N=7
	No thorns	0.80 ± 0.00 N=3	1.18 ± 0.29 N=19	1.70 ± 0.14 N=3	0.114 ± 0.011 N=3	0.42 ± 0.25 N=19	0.79 ± 0.11 N=3	18.46 ± 10.05 N=23
Cattle	Thorns	0.75 ± 0.35 N=3	1.39 ± 0.40 N=20	2.00 ± 0.00 N=3	0.057 ± 0.038 N=3	0.40 ± 0.41 N=20	1.29 ± 0.08 N=3	34.83 ± 13.85 N=8
	No thorns	0.82 ± 0.08 N=6	1.52 ± 0.60 N=64	2.77 ± 0.27 N=6	0.061 ± 0.012 N=6	0.79 ± 1.05 N=64	3.49 ± 1.38 N=6	27.05 ± 12.89 N=27

A summary of the effects of thorns on the five herbivore species is presented in Table 3. The minimum and maximum values presented in Table 3 are the 10% smallest and 10% largest twig diameters and masses selected by each herbivore. When the sample size of twigs observed to be harvested by an herbivore was less than 30, the minimum and maximum values were computed using the 3 smallest and largest values observed.

Using ANOVAs (Table 4), the herbivore species were found to differ in the twigs they harvested, and the presence of thorns differentially affected each herbivore species' harvesting ability. The results indicate: a) thorns had no effect on the number of twigs an herbivore could

harvest in a minute; b) large herbivores consumed more twigs per minute than smaller herbivores; c) large herbivores, on average, consumed twigs of larger diameter and mass; d) thorns reduced the twig diameter and mass harvested by an herbivore. Finally, thorns had a differential impact on the 5 herbivores, because the interaction terms between thorned/unthorned twigs and herbivore species in the ANOVAs for twig diameter and mass consumed were significantly different. Therefore, the effect of thorns varies with the herbivore species.

Discussion

Thorns and plants. Our results indicate that plants with thorns produce twigs of less mass than unthorned twigs of equal diameter (Fig. 1). In part, this occurs because thorned twigs of a given diameter contain less leaf mass, i.e. smaller and/or fewer leaves than unthorned twigs (Table 1). In addition, a regression of the arcsine of the proportion of twig mass composed of leaves versus thorn length provides a significant positive correlation ($r^2 = 0.40$, $N = 11$, $P \leq 0.04$).

Two factors could account for this. First, the production of thorns might be costly in terms of energy and/or nutrients, which retards the accumulation of leaf mass. Second, the reduction in leaf mass may be a second defensive strategy employed by the thorned plants, because an herbivore must consume items above a minimum mass to satisfy their nutritional requirements within limited feeding time (Belovsky 1981, 1984a, b; Schmitz 1989). Regardless of whether the reduced mass is due to

Table 4. The ANOVA results comparing the effects of thorns on herbivore food choices

Comparison	Variable	DF	F	P
Bites/min	Thorns/no thorns	1,148	1.32	0.250
	Herbivore species	4,148	18.24	0.001
	Thorns/no thorns X herbivore species	4,148	0.49	0.740
Twig diameter consumed	Thorns/no thorns	1,307	21.83	0.001
	Herbivore species	4,307	26.67	0.001
	Thorns/no thorns	4,307	5.56	0.001
	X herbivore species			
Log twig mass consumed	Thorns/no thorns	1,307	176.42	0.001
	Herbivore species	4,307	30.17	0.001
	Thorns/no thorns	4,307	10.57	0.001
	X herbivore species			

the cost to the plant for thorn production or represents a defensive strategy in itself, the twigs should be less attractive to the herbivores.

Effects of thorns on herbivore twig selection. Thorned twigs are hypothesized to affect herbivores in 3 ways. First, thorns may decrease the number of twigs harvested per minute, because the herbivore will spend time maneuvering to avoid the thorns before taking a bite. Second, thorned twigs may provide less mass at a given twig diameter. Third, thorns may decrease the twig diameter that is acceptable to an herbivore, since smaller twigs may have to be ingested to avoid the painful effects of thorns. We found that thorns affected herbivores in the second and third hypothesized ways.

There are a number of other ways that plants can be defended from herbivores. These include chemical defenses and low nutritional content (Belovsky and Schmitz 1991). For example, the high salt content of the saltbush species (*Atriplex* sp.) may help defend them from herbivores by making a certain level of consumption toxic. Belovsky and Schmitz (1991) have demonstrated that chemical defenses that are toxic to an herbivore cannot affect herbivores in the ways expected from thorns, i.e. reduced rates of harvesting plant tissues. Therefore, the effects of toxic chemicals cannot be confused with the effects of thorns. The complications of plant defenses that reduce nutritional value of the plants to the herbivores will be discussed later (e.g. chemicals that inhibit digestion and low nutritional content).

Thorns did not affect cropping times (bites/min) (Table 4). This also was found by Cooper and Owen-Smith (1986) when goats were fed twigs with thorns and twigs with their thorns removed. However, Dunham (1980) found that impala (*Aepyceros melampus*), which had previously never fed upon thorned plants, reduced their cropping rates on thorned plants. Cooper and Owen-Smith (1986) argue that this was observed because the impala were naive.

Thorned twigs, as discussed above (Discussion: Thorns and plants), have less mass at a given diameter. Also, thorns reduced the average twig size (diameter)

consumed by herbivores, but the intensity of this response differed among herbivores (Table 4). Both of the above factors would reduce the rate that thorned twig mass is ingested, which could be important for their nutritional status (Belovsky 1981, 1986; Cooper and Owen-Smith 1986).

The average twig size consumed by an herbivore, however, may not be solely a function of the presence/absence of thorns. The average twig size consumed depends upon the minimum and maximum twig sizes accepted by an herbivore, as well as the distribution of twig sizes available in the environment (Belovsky 1981, 1984a, Schmitz 1989). The distribution of twig sizes is the same for all herbivores in this study since the study was conducted at a single site. Consequently, some of the differences in average twig sizes selected by each herbivore species should be due to different minimum and maximum sizes acceptable to each herbivore species.

Larger herbivores will generally require larger minimum twig sizes, because they require greater nutritional intake (ingestion of any nutrient/time period), which means that they must ingest more food mass per unit of time than smaller herbivores (Belovsky 1986). In addition, larger herbivores will be able to consume larger maximum twig sizes, because they have larger mouths, stronger teeth, etc. This is the pattern observed (Fig. 2) and these relationships are significant for thorned and unthorned plants (no thorns: minimum - $P \leq 0.003$, $r^2 = 0.42$, $N = 20$; maximum - $P \leq 0.001$, $r^2 = 0.87$, $N = 20$; thorns: minimum - $P \leq 0.04$, $r^2 = 0.33$, $N = 16$; maximum - $P \leq 0.001$, $r^2 = 0.64$, $N = 16$).

One might suspect that the data for the largest herbivore (cattle) exerts undue influence on the regressions discussed above (Fig. 2). The statistical package SYSTAT computes leverage coefficients (Wilkinson 1990) for each observation and none indicated undue influence. No other hypothesis than herbivore body size can be envisioned to explain the patterns observed in twig diameters selected by the different herbivores. Therefore, a comparison of these minima and maxima for the different herbivores based on herbivore body mass may be important and should be examined more fully.

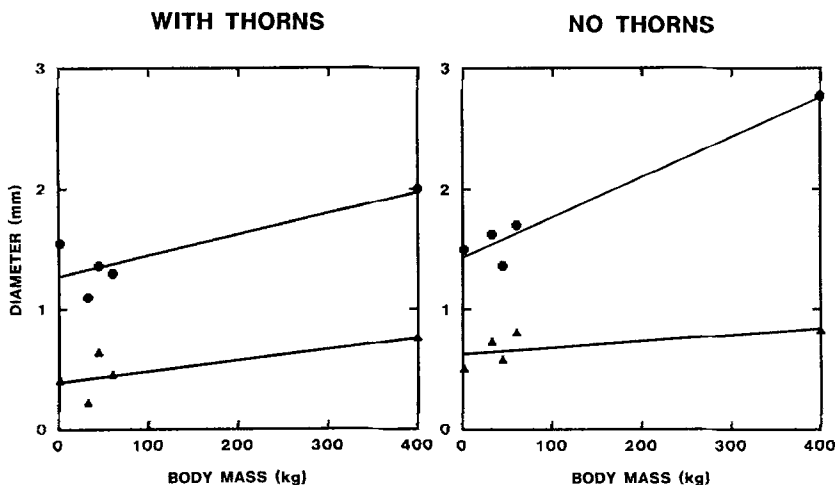


Fig. 2. The relationship between the maximum (circles) and minimum (triangles) twig sizes (based on mean values) selected by herbivores of different body masses are presented for thorned and unthorned plants. These relationships are significant (no thorns: minimum - $P \leq 0.003$, $r^2 = 0.42$, $N = 20$; maximum - $P \leq 0.001$, $r^2 = 0.87$, $N = 20$; thorns: minimum - $P \leq 0.04$, $r^2 = 0.33$, $N = 16$; maximum - $P \leq 0.001$, $r^2 = 0.64$, $N = 16$). The regression lines are also plotted

Table 5. The comparative effects of thorns on the selection of maximum twig size by different herbivores. The terms a and b refer to values from the columns marked in Table 3, ut refers to unthorned, and t refers to thorned

Herbivore	Total effect of thorns (%): [b(ut) – b(t)]/b(ut)	Do thorns reduce selected twig diameters? a(ut) vs. a(t)	Potential twig mass (g-dry) ^a	Percent reduction due to reduced mass of thorned twigs: [potential mass – b(t)]/b(ut)
Rabbit	87	no	no effect	87 ^b
Euro	80	yes	0.32	30
Red	69	yes	0.32	53
Sheep	79	yes	0.55	49
Cattle	63	yes	1.37	2

^a Unthorned twig regression from ANCOVA combining thorned and unthorned twigs (see text): g-dry mass = 0.21 (diameter in mm)^{2.79}. The equation is solved for the observed maximum twig

size selected on thorned plants by each herbivore.

^b Since thorns have no effect on diameter selected, all of change is due to reduced mass.

Maximum acceptable twig sizes should be most affected by the presence of thorns. This might be expected since twigs with a larger diameter (greater length) should have more and possibly longer thorns with which to inflict pain on the herbivore. The above regressions indicate that thorns do reduce the maximum twig sizes selected by the herbivores. Comparing the regression equations for maximum twig diameter selected versus herbivore body mass for plants with thorns and without thorns (Fig. 2), the slopes are found to be statistically different ($F = 5.46$, $DF = 1,33$, $P \leq 0.03$). First, this result indicates that the maximum acceptable twig size for an herbivore is reduced by thorns. Second, because the slopes for plants with and without thorns are different, this would indicate that herbivores of different body masses do not respond equally to the presence of thorns.

Herbivores are not equally susceptible to thorns (Table 3). We asked, for each herbivore, how much of the reduction in average twig mass ingested by each herbivore is due to the effect of thorns on twig selection, and how much is due to the reduced mass of thorned twigs? This can be done by statistically factoring out the 2 effects.

First, the observed maximum diameter for thorned twigs selected by each herbivore was substituted into the regression equation for unthorned twig diameter vs. twig mass (Fig. 1). The computed value is a hypothetical twig mass for each herbivore, which assumes thorned twigs do not have reduced mass (called "potential twig mass"). Second, the computed "potential twig mass" can be used to ascertain the effect of thorns reducing the maximum twig diameter selected by an herbivore and the effect of reduced twig mass for a given diameter on thorned plants. The impact of thorns reducing acceptable twig diameter can be measured as the difference between the observed maximum twig mass selected from unthorned plants and the "potential twig mass" for each herbivore. The impact of reduced mass for thorned twigs of a given diameter can be measured as the difference between the "potential twig mass" and the observed maximum twig mass selected from thorned plants for each herbivore.

The above differences in twig mass can be standardized as a percent reduction in maximum twig mass between thorned and unthorned twigs selected by each

herbivore (Table 5). This analysis indicates several things. First, there is no difference between the different herbivore species in the percent reduction in their maximum acceptable twig mass due to the presence of thorns (log herbivore body mass vs. arcsine transform of overall percent reduction in maximum twig mass for thorned plants: $F = 0.54$; $DF = 1,3$; $P \leq 0.52$). However, whether maximum thorned twig mass accepted by each herbivore is reduced more by the smaller maximum twig diameter accepted or the reduced twig mass at a given diameter can be ascertained. We examined this using the percent reduction in maximum acceptable twig mass due to the reduced mass of thorned twigs. These values decrease with log herbivore body mass (Table 5) ($F = 16.67$; $DF = 1,3$; $P \leq 0.027$). This means that the effect of thorns reducing the twig diameters selected by an herbivore is a better defense against large herbivores, and small herbivores are more affected by the lower twig mass of thorned plants.

Small herbivores have their selection of maximum twig diameter reduced less by the presence of thorns because of their ability to maneuver easily between the thorns when biting twigs off plants. For example, rabbits were frequently observed to move carefully between the thorns, bite off the twig, and then manipulate it in their mouth so the twig was consumed from the base. In this way the thorns were encountered from their base, minimizing the chances of being stuck by them, since thorns point outward, towards the twig's tip.

Cooper and Owen-Smith (1986) concluded that effectiveness of thorns varies with herbivore body mass, and with the degree herbivores are co-adapted with thorny plants. They concluded that large ungulates (kudu: *Tragelaphus strepsiceros*) are less affected by thorns than are small ungulates (impala and goats). In addition, they cite data on giraffe (Pellew 1984) and black rhinoceros (*Diceros bicornis*) (Guggisberg 1966) to substantiate this. However, none of these studies apportioned the effects of thorns in reducing the twig diameter selected and reducing the twig mass of thorned plants.

In addition, our results suggest that non-coadapted herbivores are no more affected by thorns than co-adapted herbivores, since the kangaroos (native) and sheep (introduced) have similar body sizes and are equally

influenced by the thorns. Interestingly, since thorn effectiveness per se is greater on larger herbivores than kangaroos, thorns evolved either for reasons other than an anti-herbivore defense, or they evolved in response to larger marsupial herbivores that became extinct in the late Pleistocene (Hope 1982, also see Myers and Bazely).

Minimum acceptable twig sizes, if influenced by thorns, might be expected to be larger than for unthorned plants to compensate for the reduced maximum sizes of thorned twigs accepted by the herbivores. However, the results presented above indicate that the herbivores select smaller minimum twig sizes on thorned plants (Fig. 2: $F = 13.22$, $DF = 1,35$, $P \leq 0.001$). Furthermore, the slopes of the regression equations for thorned and unthorned minimum twig diameters selected by the herbivores of different body masses are not statistically different. This indicates that the mechanism for the selection of the minimum acceptable twig diameter is the same for each herbivore, regardless of body mass and the presence/absence of thorns.

A common mechanism might be nutritional intake considerations for each herbivore. As presented above, plant toxicity should have no influence on item size selection (Belovsky and Schmitz 1991), but nutritional value can influence item size selection. Nutritional value can vary with nutrient content and digestibility, which is influenced by the plant's structural components and digestive-inhibiting chemicals (Belovsky 1981). We do not believe that these herbivores' food selection is based upon the protein content of the vegetation, since at the time of the study, the vegetation averaged 23.3% crude protein with woody plants averaging 16.4% (Koteles pers. comm.). These crude protein values are very high and well above values thought to be limiting herbivore nutrition. Furthermore, from other studies conducted by us at this site (Belovsky, Schmitz, Slade and Dawson, unpublished data) energy intake appears to be the currency sought by the herbivores in their plant selection.

Based upon nutritional considerations, Belovsky (1981, 1984a, b, 1986) found that the minimum plant item size selected by an herbivore (I : g-dry/item) could be estimated as:

$$I = M/(TCKD),$$

where M is the herbivore's metabolic requirement of some nutrient (quantity/day), T is the herbivore's maximum daily feeding time (min/day), C is the number of items the herbivore can harvest per unit of time (items/min), K is the gross nutrient content of the food (quantity/g-dry), and D is the proportion of gross nutrient content that is assimilated.

We know that the number of items harvested per unit time (C) for thorned and unthorned plants is the same (Table 4). We should not expect an herbivore's maximum feeding time (T : min/day) or its metabolic requirements (M : KJ/day) to change whether thorned or unthorned plants are eaten. Feeding time is probably set by the herbivore's ability to be active at different times of the day when its alimentary tract is not full and thermal conditions are tolerable. Metabolic requirements are set

by the herbivore's nutritional requirements for maintenance.

Plants generally vary less in their gross energetic value (K), than in the proportion that is assimilated by the herbivore (D). Therefore, the proportion of energy in the plants that can be assimilated (D) is the most likely parameter varying between thorned and unthorned twigs that could cause the observed differences in minimum twig size selected. This would indicate that D for thorned plants is greater than for unthorned plants.

D depends upon the herbivore's choice of individual plants and plant parts; it is not a simple measure of plant chemistry. D can be written as (Belovsky 1981, 1984a, 1986):

$$D = MB/(SFK),$$

where B is the food's fill of the herbivore's alimentary tract (bulkiness: g-wt/g-dry), S is the herbivore's alimentary tract capacity (g-wet), and F is the number of times the herbivore's alimentary tract can be filled each day (X 's/day). For D to be greater for thorned plants ($D_t > D_u$), the product, $B_t F_u$, must be greater than the product, $B_u F_t$, since the values that remain constant for thorned or unthorned plants will cancel from the equation (M , S , K).

B_t is 1.05 times greater than B_u (2.3 ± 0.4 , $N = 5$ species, vs. 2.2 ± 0.4 , $N = 4$ species), as expected. The number of times that the herbivore's alimentary tract can be filled each day (F) by thorned versus unthorned plant tissues cannot be ascertained as simply. Plant tissue high in fiber is retained in the alimentary tract longer by these herbivores (S. McCloud, pers. comm.). We know that the thorned twigs have less leaf tissue per unit mass than unthorned twigs (Table 2); this indicates that thorned twigs have more stem, the portion of the twig that is highest in fiber, and, consequently, F_t should be less than F_u . The chemical solubility studies (Table 2) support this since the unthorned plants are more soluble (less fiber) ($53.7\% \pm 11.7$, $N = 4$ species, vs. $36.8\% \pm 0.5$, $N = 5$ species). The results suggest that F_u should be approximately 1.5 times greater than F_t .

The above comparison of the thorned and unthorned plant characteristics ($B_t F_u$ vs. $B_u F_t$) would indicate that the minimum twig size for thorned plants should be 1.6 times smaller than that for unthorned plants. The observed difference based upon a comparison of the intercepts in Fig. 2 is 1.7. Therefore, it appears that simple nutritional traits of thorned and unthorned plants explain the differences in the herbivores' selection of minimum twig sizes.

Conclusion

The results of this study indicate that plants defended by thorns and spines are actually employing two anti-herbivore strategies. Thorns and spines reduce the maximum twig diameter that each herbivore selects, and thorned twigs of a given diameter have reduced mass at a given diameter because they possess less leaf mass. Both

of the defenses reduce the acceptability of the defended plants to herbivores because the defenses reduce the ability of the herbivore to ingest food mass per unit of time. However, thorns and spines do not appear to influence the herbivore's harvest rate (twigs/time).

While all 5 of the herbivores studied were equally affected by the defenses in toto, they were differentially affected by each of the two modes of defense. The above results indicate that different herbivores can be differentially affected by the plant defenses posed by thorns and spines, and reduced twig mass. Therefore, before we can assess the effectiveness of thorns as defenses, we must examine both factors. This may explain the inconsistent results reported on the efficacy of thorns and spines as plant defenses (Cooper and Owen-Smith 1986, Myers and Bazely in press).

A closer examination of how these defenses influence the maximum and minimum twig sizes that each herbivore is willing to ingest indicates an even more complex situation, which can only be understood using foraging models. Using foraging theory to unravel how plant defenses can be effective against herbivores (Belovsky and Schmitz 1991) indicates that defenses are not always effective.

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