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Effects of plant defenses and water availability on seasonal foraging preferences of the Nubian Ibex (*Capra nubiana*)

Elsita M. Kiekebusch * and Burt P. Kotler

Mitrani Department for Desert Ecology, Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Midreshet Ben-Gurion, Israel

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The study of herbivore patch use has implications for herbivore habitat quality assessment, foraging behaviors, species interactions, and coexistence in patchy environments. This research focuses on the comparison of the effects of two qualitatively different plant defenses, mechanical (thorns) and chemical (tannins), on ibex foraging preferences during different seasons of the year. The occurrence of both chemical and mechanical plant defenses were experimentally manipulated in artificial resource patches, in addition to water availability. Ibex foraging preferences were quantified using giving-up densities during four separate fieldwork sessions in each of the seasons of the year at cliff sites overlooking the Zin Valley of the Negev Highlands. Both mechanical and chemical plant defenses significantly hindered ibex food intake overall. Mechanical and chemical defenses acted as substitutable defenses, meaning that their combined effects were not greater than additive. There were strong seasonal patterns of the amount of food consumed by ibex, further corroborated by comparison to rainfall levels. Seasonality also interacted with the effectiveness of plant defenses. Thorns were especially ineffective in summer, whereas tannins were most effective in spring. Decreases in seasonal food availability and increased marginal value of energy for ibex may have resulted in thorn ineffectiveness, while seasonal changes in the emergence of young foliage may have resulted in the greater springtime tannin effectiveness. Water was not found to mitigate the detrimental effects of tannins through dilution. The implications for decreased constraints on selective pressures on ibex due to the substitutability of plant defenses are discussed.

Keywords: foraging behavior; herbivore patch use; Nubian Ibex; giving-up density; plant defenses; resource complementarity

Introduction

The use of resources by foragers has been described as an optimization process shaped by natural selection (MacArthur & Pianka 1966). When optimizing patch use, foragers must decide how long to stay in a patch before moving to another in a manner that maximizes the ratio between foraging benefits from food harvested and costs of foraging as arising from predation risk, energetic losses, and missed opportunities from other activities (Brown 1988). In addition, herbivore foragers must contend with plant defenses – mechanisms evolved by plants to deter herbivory. These defenses can be mechanical, for example thorns that can cause injury or increase the handling time of food items by foragers (Cooper & Owen-Smith 1986; Wilson & Kerley 2003). Plant defenses can also be chemical, involving the production of secondary compounds such as polyphenols (including tannins), alkaloids, saponins, and terpenoids that may function as toxins or “digestibility reducers” (Schmidt 2000) to herbivores. Ward et al. (1997) demonstrated the effectiveness of oxalates as a chemical defense against gazelle herbivory. Two different resources, such as food and water, may show a nutritional interaction such that the value of one depends on how much of the other has been consumed. A complementary interaction is defined as that in which the benefit of consuming two food resources together is

greater than that of consuming them separately (León & Tumpson 1975; Schmidt 2000). Thus, the presence of both resources will cause an increase in the exploitation of the food patch. Likewise, an antagonistic interaction is when the opposite is true and the presence of both resources causes a decrease in the exploitation of the resource patch.

Nubian Ibex (*Capra nubiana*) are wild goats that are seen in mountainous rocky desert areas of the Middle East. Ibex are diurnal, foraging during early morning and late afternoon hours (Levy & Bernadsky 1991). They are unlike many desert-dwelling herbivores in that they require daily water intake. Ibex eat a wide variety of herbaceous and woody plants (Alkon et al. 2008). They prefer to graze on annual vegetation and browse most Negev Desert perennial species (Alkon et al. 2008). Seasonally, ibex change their plant species preferences and have been observed to increase consumption of alkaloid-producing plants in June when other food is scarce (Hakham & Ritte 1993). Five “principal” food species have been identified: *Acacia raddiana*, *Moringa peregrina*, *Ziziphus spinachristi* (trees), *Salsola vermiculata* (shrub), and *Pennisetum asperifolium* (perennial grass) (Hakham & Ritte 1993). In particularly rainy winters, ibex grazed an additional 15 annual species, and they also consumed *Zygo-phyllum dumosum*, *Salvadora persica*, and *Pennisetum*

*Corresponding author. Email: emkiekeb@ncsu.edu

ciliare in other parts of the year (Hakham & Ritte 1993). Plants growing in nutrient-poor soils have been shown to invest heavily in anti-herbivore defenses (Coley et al. 1985). *Acacia raddiana* invests simultaneously in thorns and tannins, and has been shown to increase production of both defenses under increasing levels of herbivore browsing (Rohner & Ward 1997).

Nutritionally, proteins increase food quality for ibex (Kotler et al. 1994). In addition, tannic acid decreases food quality (Hochman & Kotler 2006a) likely because tannins decrease digestibility and assimilation of protein in ruminants (Cooper & Owen-Smith 1985; Robbins et al. 1987; Rubanza et al. 2005). Dearing et al. (2002) note that especially for herbivores living in arid environments, water is necessary for the excretion of detoxified plant secondary compounds. The complementarity of food and water has been shown for Nubian Ibex in summer (Hochman & Kotler 2006a), as well as for other desert-dwelling herbivores including Australian ravens (*Corvus coronoides*; Kotler et al. 1998) and goats (*Capra aegagrus*; Shrader et al. 2008), but not for species such as klip-springer (*Oreotragus oreotragus*; Druce et al. 2009) and sandy inland mouse (*Pseudomys hermannsburgensis*; Kotler et al. 1998).

We examined the interactions of mechanical and chemical plant defenses for Nubian Ibex in the context of the complementarity of food and water. To this end, the occurrence of both chemical and mechanical plant defenses were experimentally manipulated in artificial resource patches, along with the availability of water during each of the four seasons of the year. The objective of the research was to determine the effects of the mechanical and chemical defenses, water availability, their interactions, and how these change seasonally, on the patch use behavior of Nubian Ibex.

Quantifying Nubian Ibex foraging behavior

Charnov's (1976) marginal value theorem predicts how long a forager should exploit a resource patch. It assumes that the forager incurs a constant risk of predation, that it has complete knowledge of patch locations, travel times, and patch values, it cannot deplete the environment, it can only choose between exploiting the current patch or traveling to a new patch, and its foraging activity in the current patch causes patch depletion and diminishing returns. The theorem predicts that a forager will stay in the patch until its instantaneous harvest rate in the patch (the patch's marginal value) drops to the average value of all patches in the environment. At this point, it is beneficial for the forager to find a new patch. The marginal value theorem predicts that in a rich environment foragers will remain in resource patches for less time than in a poorer environment, but that in the same environment they will exploit rich patches longer than poor patches. Brown (1988) builds on the marginal value theorem by relaxing these assumptions and demonstrating that a forager facing risk of predation and foraging in a depletable environment should remain in the patch until its quitting harvest rate (H) is equal to its energetic (C), predation (P), and missed

opportunity costs (MOC) of foraging.

$$H = P + C + \text{MOC} \quad (1)$$

The resource density at the point where this equation is true is called the giving-up density (GUD), i.e., the amount of food left in the patch when the forager quits harvesting. This value is thus an indicator of the forager's perception of its risk of predation, energetic state, and environmental quality. Brown (1988) introduces the technique of using GUDs in experimental food patches to investigate habitat preferences, predation risks, and inter-specific competition. An experimenter can create artificial resource patches by mixing a pre-measured amount of food into a feeding tray filled with inedible substrate (sand, plant litter, etc), thus creating diminishing returns of resource harvest over time (Brown 1988; Kotler & Brown 1990). The use of such artificial food patches permits experimental manipulation while also allowing foragers to remain in their natural environment.

Similar to the interaction between resources such as food and water, Schmidt et al. (1998) define the interaction between two kinds of plant defenses as complementary, antagonistic, or substitutable. For defenses to be perfectly substitutable, the rate with which one defense can be substituted for another (the marginal rate of substitution) without changing a forager's fitness is constant. In other words, combining foods with substitutable defenses has an additive effect on the fitness of the herbivore. However, if relative to perfect substitutability, a mixed diet increases a forager's fitness, the defenses are said to be complementary. This can occur when the effect of one defense cancels the effect of the other. Plant defenses are said to be antagonistic if, relative to perfect substitutability, a mixed diet decreases fitness. This can occur when the effect of one defense enhances that of the other. Schmidt et al. (1998) show that the interaction between two defenses can be revealed by providing a freely available augmentation of food protected with a single defense alongside a choice of defended GUD trays. The herbivore consumes the entire augmentation because it is not subject to diminishing returns ("free"). Afterwards, whether the herbivore consumes more of the food protected with the first defense, food protected with the second defense, or equivalent amounts of the two reveals if they are antagonistic, complementary, or substitutable, respectively.

Based on Brown (1988) and Schmidt (2000), Shrader et al. (2008) redefine Equation (1) to incorporate the effect of plant secondary compounds (T):

$$H - T = C + P + \text{MOC} \quad (2)$$

Equation (2) shows that the harvest rate of the forager decreases because plant secondary compounds reduce food quality. If availability of water (W) improves the quality of the food, the quitting harvest rate should be positively affected (Shrader et al. 2008).

$$H - T + W = C + P + \text{MOC} \quad (3)$$

If water mitigates the harmful effect of the plant secondary compounds, the foraging cost of the secondary compounds ($T(W)$) declines with increasing water availability (Shrader et al. 2008).

$$H = C + P + T(W) - W + \text{MOC} \quad (4)$$

Finally, if thorns increase foraging costs by increasing the handling time of foraging, then the quitting harvest rate becomes a function of plant mechanical defenses (M).

$$M(H) = C + P + T(W) - W + \text{MOC} \quad (5)$$

Thus, by measuring GUDs as estimates of quitting harvest rates, the experimental manipulation of thorns, tannins, and water in an artificial resource patch can demonstrate the effects and interactions of these variables.

Based on the theory presented above and on previous research (Hochman 2004; Hochman & Kotler 2006a; Tadesse 2008) on Nubian Ibex of the Negev, we predict that plant defenses will reduce food quality for ibex and thus GUDs will increase with both the artificial treatments of thorns and tannins. We also predict that thorns and tannins are antagonistic defenses. The presence of a tannin augmentation will increase the GUDs from thorn-treated artificial resource patches relative to GUDs found in patches without tannin augmentation. Seasonality will change the effectiveness of plant defenses. For example, in summer when food is less available in the environment, the GUDs of tannin or thorn-treated patches will be closer in amount to control patches whereas in winter, GUDs in treated patches will increase relative to control patches. We predict that food and water are complementary resources for ibex across all seasons, meaning that GUDs will decrease when water is available. Similarly, seasonality will affect the complementarity of food and water. For example, in summer when water is less available in the environment, the GUDs of water-augmented patches will decrease relative to the GUDs found in winter. We predict that water will mitigate the effect of tannins by assisting their excretion in detoxified form. GUDs in tannin-treated artificial resource patches with water will decrease compared to patches without water. This will also be manifested by a seasonal effect on tannins, with tannins being more detrimental when water is limited (summer).

Methods

Experiments

The research was carried out near Midreshet Ben-Gurion, along the cliffs of the Zin Valley in the Negev Desert of Israel – Study Area (box): 30°51'5.71"N, 34°47'27.82"E to 30°51'9.25"N 34°47'34.46"E – within the confines of the Zin Nature Reserve. The area is characterized by the ephemeral river, tributaries, and drainage of the Nahal Zin, steep rocky canyons, loess plains, and plateaus (Gross et al. 1995). The regional elevation varies between 320 and 580 m a.s.l. As a hyper-arid zone, by definition the area receives less than 100 mm of rain per year causing high

variation in biomass production spatially and annually (Schulze et al. 1980). Rainfall occurs mostly during winter.

We examined the interaction between mechanical and chemical plant defenses, the complementarity of food and water and plant defenses, and the effect of seasonality using the GUD technique (Brown 1988; Kotler & Brown 1990). Ibex were presented with artificial resource patches: 46 × 30 × 12 cm wooden trays filled with inedible substrate and pre-measured amounts of food. The food consisted of 100 g of rodent pellets produced by Koffolk Ltd. The inedible substrate was created by filling the trays with 1400 g of black plastic irrigation tubes (1 cm diameter) cut into 3 cm lengths. Trays were covered with chain-link fencing, forcing ibex to insert their muzzles into each link in a manner similar to animals reaching for interior shrub leaves (Kotler et al. 1994). This setup caused the foraging ibex to experience diminishing returns to resource harvest over time spent foraging, prompting them to choose to leave the patch when their harvest rates dropped below their foraging costs (Kotler & Brown 1990).

We simulated plant chemical defenses by soaking food pellets in a solution of 1 g reagent grade tannic acid (Sigma-Aldrich Co.) per 10 ml of distilled water, following Schmidt et al. (1998). Pellets were soaked for 30 min allowing the solution to be absorbed. Afterwards, pellets were oven-dried at 60 °C for 24 h. As a control for the tannin treatment, a second group of pellets were soaked in distilled water, the amount of which corresponded to that of the tannic acid solution. Because the distilled water was absorbed more quickly than the tannic acid solution, control pellets were soaked for 10 minutes. Pellets were then oven-dried at the same temperature for the same duration. Pellets that were soaked in tannic acid solution had a similar consistency and texture as the water-soaked pellets, but unlike the control, they also showed a slight color change.

We recreated the plant mechanical defenses by attaching several rows of thorny acacia branches to the chain-link of the feeding trays. Shorter thorny acacia branches were also mixed in with the inedible substrate. As a control for the thorn treatment, we attached smooth branches of a similar length to the chain-link of control trays, and also mixed them with the inedible substrate in a manner similar to the thorn treatment.

We placed four feeding trays at each of eight stations in the field. Stations were situated 30 m apart and within 5–10 meters of the cliff edge based on the knowledge that ibex perceive proximity to the cliffs as safety (Kotler et al. 1994, Hochman & Kotler 2006b). Food was placed in trays at stations every morning around the time of sunrise, and the amount of leftover food (the GUD) was collected from trays at sunset for weighing, such that one day constituted a single foraging session. This time period was chosen based on the knowledge that ibex are solely diurnal foragers, and it also prevented foraging by nocturnal species such as porcupines (*Hystrix indica*) from affecting the GUDs. We spread sand around each tray to allow the identification of animal tracks and to verify that only ibex foraged from the trays during foraging sessions.

Tray setup followed a factorial arrangement where at each station there were two tannin trays (food pellets

soaked in tannic acid) and two tannin control trays (food pellets soaked in water) crossed with two thorn trays and two smooth-branched control trays. The interaction between thorns and tannins was tested following the method of Schmidt et al. (1998), using the provision of a tannin augmentation. That is, in addition to that in the wooden trays, 200 g of tannin-soaked food pellets were provided at each station in a 25 × 20 × 10 cm plastic tub on half of the experimentation days. We expected that the ibex would eat all of the tannin augmentation because it was freely available (no chain-link or inedible substrate to reduce harvest rates in the trays). With tannin augmentation, the relative amounts of food consumed from the assessment trays under the two treatments would then reveal the nature of the interaction between the two defenses.

In order to test for the complementarity of food and water, a water augmentation was provided alongside the trays at each feeding station on half of the experimentation days. This augmentation consisted of 1 L of tap water in a plastic tub. The complementarity of food and water has been shown for ibex during the summer months (Hochman & Kotler 2006a). This research thus repeats this experiment and also tests for complementarity during the other seasons of the year. This experimental setup also allowed us to test for interactions between tannins and water. For example, if ibex consume more tannin-soaked pellets in the presence of water, it would suggest that water mitigates the negative effects of tannins.

In order to test for the effect of seasonality, the experiment was repeated in each of four seasons: spring (May 2011), summer (August 2011), fall (November 2011), and winter (February 2012). Pre-measured food was placed in the trays two days out of every three over a period of 18 days for a total of 12 experimental days per season. The placement of each of the trays at a station was rotated in space and time following a Latin-square arrangement. Data collected consisted of the measured giving up densities from each wooden tray along with its categorical treatments. Data were analyzed by repeated measures ANOVA including all variables using Systat software version 13. Figures were created using the R software environment.

Tannic acid amount

The amount of tannic acid per dry mass of rodent pellets is calculated below. A solution of tannic acid was created by adding 200 g of reagent grade tannic acid ($C_{76}H_{52}O_{46}$) to 2000 ml of distilled water (1 g per 10 ml) following Schmidt et al. 1998. This amount of solution was distributed amongst five baking trays, each containing a layer of rodent pellets. After allowing the solution to soak into the pellets for 30 min, the trays and their contents were oven-dried at 60 °C for 24 h. The resulting tannin-soaked pellets weighed on average 700 g per tray.

$$\begin{aligned} \text{Amount tannic acid added} &= 200 \text{ g tannic acid} / (5 \times 700 \text{ g pellets}) \\ &= 0.0571 \text{ g tannic acid/g rodent pellets} \\ &= 57.1 \text{ mg/g rodent pellet} \end{aligned}$$

By way of comparison, this amount is more than double the amount of protein precipitating tannins found in leaf samples of *A. raddiana*: 26.72 mg tannic acid equivalent/g dry mass (Rohner & Ward 1997).

Rainfall data

Rainfall data were collected daily at Midreshet Ben-Gurion by the Meteorology Unit of the Department of Solar Energy and Environmental Physics, at the Blaustein Institutes for Desert Research (Zangvil et al. 2012). Data were summarized by seasons (Table 2) for further comparison with seasonal experimental results.

Comparison of pellet types

Due to a change in pellet brand availability, three different kinds of pellets were used during the course of the experiment. During the first experimental season (May), pellets produced by Koffolk Ltd (Pellet Composition 19520; 21% protein) were used. During August, pellets produced by Harlan Laboratories (Teklad Certified Global 18% Protein Rodent Diet) were used. During November and February, pellets produced by Altromin Spezialfutter GmbH & Co (1324 Fortified Maintenance Diet; 19% protein) were used. All pellet types were approximately the same size (1 × 2 × 0.5 cm) and they absorbed the same amount (all) of the tannic acid solution in which they were soaked.

Pellets were compared in two separate experiments in order to test for differences in ibex preference for the different pellet brands. In the first experiment, Koffolk pellets were compared to Harlan pellets during early August. At each of five experimental stations, ibex were presented with two patches of Koffolk pellets and two patches of Harlan pellets. The experiment was carried out for three days prior to the main experiment days. In the second experiment, all three of the pellet brands were compared during early November. At each of five stations, ibex were presented with one patch of Koffolk pellets, one patch of Harlan pellets, and one patch of Altromin pellets. The fourth artificial resource patch was covered. The experiment was carried out for three days prior to the main experiment days. Differences in resulting GUDs were statistically compared for both experiments.

Results

Interactions between season, plant defenses, and water

Data were collected in four sessions from May 2011 to February 2012, corresponding to spring, summer, fall, and winter seasons. All data were analyzed together to examine seasonal effects ($N = 1435$, $R = 0.723$, $R^2 = 0.522$; Table 1), and Tukey honest significant difference (HSD) post-hoc tests were used to examine differences within treatment effects and within interactions with multiple variables. There was a significant seasonal difference in amount of pellets consumed, with ibex consuming most pellets in summer, followed by fall and winter, and consuming the least during spring (Table 1, Figure 1). This

Table 1. Results of ANOVA testing effects of season, plant defenses, water augmentation, tannin augmentations, and interactions on ibex GUDs.

Factor	df	Mean square	F ratio	P
Season	3	23,184.596	8.386	0.007
Thorn	1	2609.049	17.081	<0.001
Tannin	1	10,588.840	69.324	<0.001
Water	1	1500.042	0.543	0.467
Tannin augmentation	1	13,832.065	5.003	0.032
Season*Thorn	3	648.742	4.247	0.005
Season*Tannin	3	877.013	5.742	0.001
Season*Water	3	2286.393	14.969	<0.001
Season*Tannin augmentation	3	2502.838	16.386	<0.001
Thorn*Tannin	1	12.199	0.080	0.778
Thorn*Water	1	57.543	0.377	0.539
Thorn*Tannin augmentation	1	85.099	0.557	0.456
Tannin*Water	1	371.191	2.430	0.119
Tannin*Tannin augmentation	1	0.208	0.001	0.971
Water*Tannin augmentation	1	455.596	2.983	0.084
Season*Thorn*Tannin	3	102.299	0.670	0.571
Season*Thorn*Water	3	95.451	0.625	0.599
Season*Thorn*Tannin augmentation	3	588.107	3.850	0.009
Season*Tannin*Water	3	246.580	1.614	0.184
Season*Tannin*Tannin augmentation	3	462.195	3.026	0.029
Season*Water*Tannin augmentation	3	631.559	4.135	0.006
Thorn*Tannin*Water	1	20.985	0.137	0.711
Thorn*Tannin*Tannin augmentation	1	0.526	0.003	0.953
Thorn*Water*Tannin augmentation	1	105.846	0.693	0.405
Tannin*Water*Tannin augmentation	1	360.760	2.362	0.125
Day (Season*Water*Tannin augmentation)	32	2764.644	18.100	<0.001
Error	1355	152.744		

seasonal pattern of consumption suggests a reflection of rainfall patterns and resultant available vegetation in the environment.

Plant defenses affected patch use in ibex. Overall, ibex consumed more pellets in the absence of thorns than in their presence (Table 1), demonstrating that this mechanical plant defense deters herbivory. Similarly, the chemical defense also deterred ibex from foraging. Ibex consumed

more pellets in the absence of both tannins and the tannin augmentation than in their presence (Table 1).

Season interacted significantly with each of the main variables (Table 1). Interactions between season and thorns (Figure 2) revealed that thorns deterred ibex the most in the spring when food was most abundant ($p = 0.001$, Tukey HSD). At this time, thorns significantly increased the GUDs of ibex, but in summer, when food

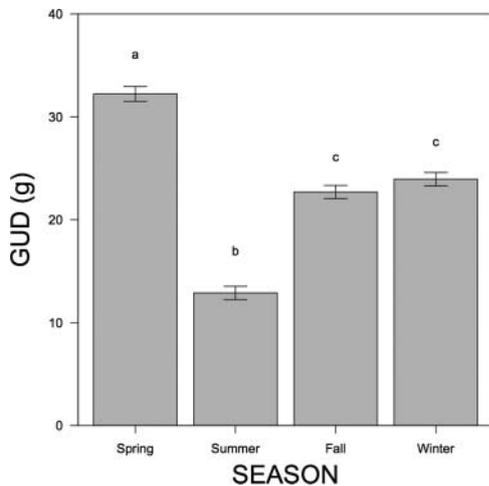


Figure 1. Changes in GUD over seasons. Error bars represent standard error of the mean.

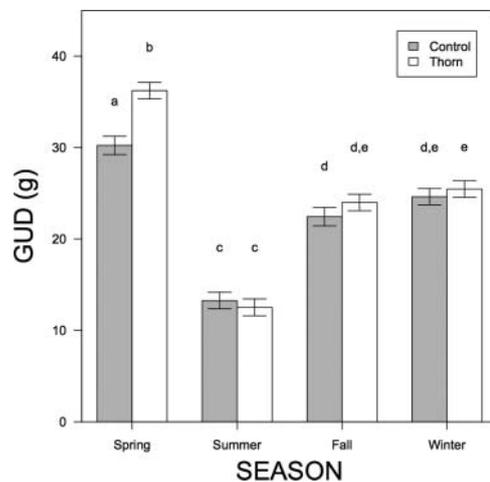


Figure 2. Interaction between season and thorns. Error bars represent standard error of the mean.

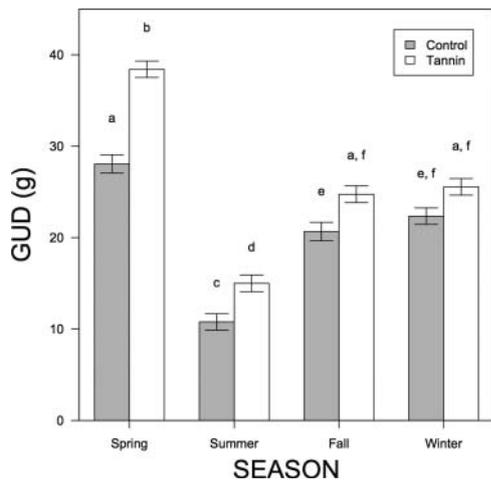


Figure 3. Interaction between season and tannins. Error bars represent standard error of the mean.

was least abundant, the presence of thorns did not influence ibex GUDs ($p = 0.999$, Tukey HSD). In fall and winter, there was an increasing trend in GUDs with the presence of thorns, but this was also not significant.

Interactions between season and tannins (Table 1, Figure 3) were significant. Whereas thorns strongly deterred ibex only in spring, the presence of tannins increased GUDs in three seasons ($p < 0.001$ for spring, $p = 0.022$ for summer, and $p = 0.029$ for fall, Tukey HSD). In winter, the increase was not significant ($p = 0.202$). Thus, even when food was scarce in summer, tannins were still effective defenses. Similarly, season also interacted significantly with the augmentation of tannin (Table 1, Figure 4). The presence of a free tannin augmentation raised ibex GUDs in spring and summer ($p < 0.001$ for spring and $p < 0.001$ for summer, Tukey HSD), but not in fall and winter.

The effect of water on GUDs showed strong seasonal variation (Figure 5). In the spring, the presence of water decreased GUDs though the interaction was marginally significant ($p = 0.063$, Tukey HSD.) In the following season, this effect was changed such that water significantly

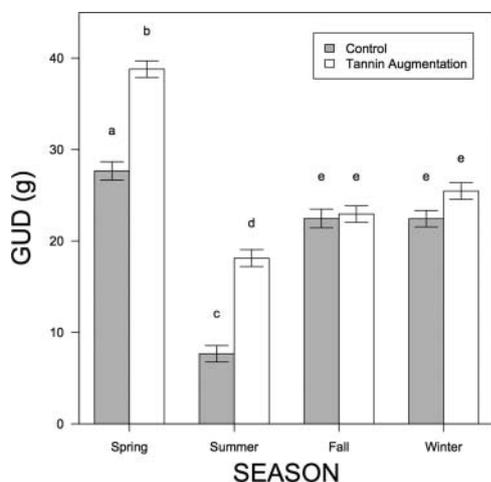


Figure 4. Interaction between season and tannin augmentation. Error bars represent standard error of the mean.

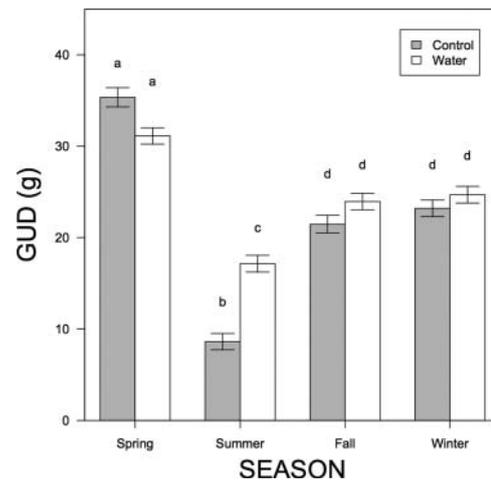


Figure 5. Interaction between season and water availability. Error bars represent standard error of the mean.

increased GUDs during the summer ($p < 0.001$). During the fall and the winter, changes in GUDs were not significant ($p = 0.513$ for fall and $p = 0.945$ for winter). These results explain why, on average across all seasons, the presence of water alone did not alter GUDs.

Ibex readily consumed all of the freely available tannin augmentation at all stations on all days except on three separate occasions, a necessary condition for the comparison of the two plant defenses. This negated any need for data analysis comparing the amounts of tannin augmentation left unconsumed. The statistical analysis revealed that thorns and tannins are substitutable defenses for ibex: there was no significant change between the relative GUDs of thorn-treated, tannin-treated, thorn-and-tannin-treated, and control patches in the presence vs. absence of the tannin augmentation (Figure 6).

Additionally, there were several significant three-way interactions (Table 1). The interaction between season, thorns, and tannin augmentation revealed that tannin augmentation increased effectiveness of thorns in spring, but not in winter. However, there was no seasonal interaction between thorn and tannin, so the importance of this result

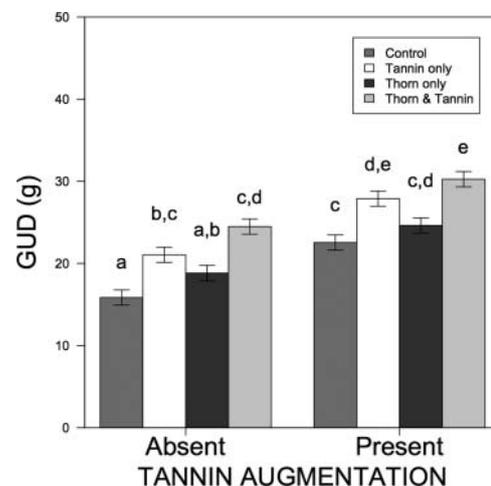


Figure 6. Interaction between thorns and tannins in the presence or absence of tannin augmentation. Error bars represent standard error of the mean.

Table 2. Cumulative three-month seasonal rainfall (mm) up to and including relevant months of data collection.

Date	Rainfall (mm)
(Winter) December, January, February 2010–2011	29.3
(Spring) March, April, May 2011	14.4
(Summer) June, July, August 2011	0
(Fall) September, October, November 2011	2.6
(Winter) December, January, February 2011–2012	17.5
Total	63.8

may be lessened. Season, tannin and tannin augmentation also interacted significantly (Table 1), revealing that tannins were most effective in spring. These results directly corroborated the season by tannin interaction (Figure 3). The three-way interaction between season, water, and tannin augmentation was also found to be significant (Table 1). Water did not affect ibex preference except in summer in the presence of the tannin augmentation, which may be due to an increase in environmental quality due to both augmentations.

Rainfall data

Data are summarized in Table 2, showing seasonal rainfall from winter 2010–2011 through winter 2011–2012.

Pellet analyses

In the first experiment, conducted in August, we compared Harlan pellets, used in August, with Koffolk pellets, used in May. Ibex showed similar GUDs on these pellets ($df = 1$, $F = 0.371$, $p = 0.545$). In the second experiment, conducted in November, we placed compared Harlan, Koffolk and Altromin pellets, used in November and February. Ibex showed significantly different GUDs according to pellet type ($df = 2$, $F = 4.890$, $p = 0.013$). Tukey's HSD showed that ibex had lower GUDs on the Harlan pellets than on the Altromin pellets ($p = 0.013$), but that GUDs on Koffolk were not significantly different from either Harlan ($p = 0.078$) or Altromin ($p = 0.724$). Thus, some of the seasonal variation can be attributed to the unforeseen necessity of using different pellet types in the different months, but the results of the within-season comparisons were not affected by the differences in pellet type. This result suggests that protein content did not play a role in ibex pellet choice where for example the Harlan pellets had the lowest protein content (18%) and the lowest GUDs compared to Koffolk (21%) and Altromin (19%).

Discussion

Seasonal effects

Seasonal comparisons revealed significant differences in ibex GUDs during different times of the year (Figure 1). Seasonal changes in GUDs reflected general predictions. In August, GUDs were lowest, conforming to the general

hypothesis that during seasons of low water and food availability when marginal values of energy are highest and MOC of foraging lowest, ibex should leave less food behind in trays. However, during winter, which was previously assumed to have lowest marginal values of energy due to food availability and winter rains, the GUDs did not increase to a greater level than those of spring. This may be partly explained by the fact that the 2011/2012 winter season was particularly dry. By comparison, the previous winter experienced 11.8 mm more rainfall (Table 2). The winter months leading up to and including February 2012 achieved only somewhat greater rainfall than the spring months leading up to and including May 2011. A dryer winter would lead to a decrease in available vegetation, thus increasing the marginal value of energy for the ibex. This in turn would lead to a lower level of GUDs than expected. Stuart and Stuart (2000) note that most offspring are born in March. Therefore, the marginal value of energy for female ibex would be increased during February when they would need more energy during gestation leading to decreased GUDs. Upon giving birth, this energy would be converted directly into offspring and the marginal value of energy would drop immediately thereafter leading to increased GUDs in spring. Similarly, the impact of the September/October mating season (Stuart & Stuart 2000) could have led to increased marginal value of energy for males needing to increase their body mass prior to the rutting season contributing to the decrease in summer GUDs. Further investigation is needed to tease out the effects of ibex reproductive costs on marginal values of energy for male and female ibex at relative times of the year.

Plant defenses

Mechanical vs. chemical defenses

The results demonstrate that both types of plant defenses reduced the food quality of a resource patch. It is not surprising that tannins decreased food quality for ibex, as it has been previously demonstrated for ibex at Midreshet Ben-Gurion (Hochman & Kotler 2006a). However, this is the first time these results have been shown empirically for ibex with mechanical defenses, and they set the scene for further qualitative comparison between mechanical and chemical defense. Much of the previous literature has dealt with substitutability and complementarity of resources in terms of foragers optimizing nutritional gains (Rapport 1980; Pennings et al. 1993) as opposed to minimizing the costs due to defenses. Based on the definition by Schmidt et al. (1998), we were able to demonstrate that thorns and tannins are substitutable defenses. Compared to complementarity and antagonism, substitutability of defenses constrains ibex foraging choices the least. If plant defenses were complementary, it would benefit ibex to seek and consume different plants with a greater variety of defenses (Schmidt et al. 1998) potentially forcing ibex to disperse more widely, increasing both search time (C) and cost of predation (P). Substitutability negates these potential costs for ibex. These results also suggest the

applicability of a traditional approach to optimal foraging in which resources are identical and thus can be valued and ranked by a single currency such as energy (Schoener 1971). This would suggest that ibex rank resources by their nutritional and energetic needs, foraging on the variety of plant species necessary to obtain an optimal diet instead of being limited by the type of defense. Additionally, the complementarity of available plant resource types (if it exists) would play an important role in foraging decisions of ibex. Schmidt et al. (1998) also point out that complementarity of plant defenses, by increasing the fitness of a forager who consumes resources with both defenses relative to consuming one or the other, would constrain foragers to be generalists. Similarly, antagonism of defenses, by decreasing the fitness of a forager that consumes both resources together, would constrain foragers to be specialists. Substitutability places no such constraints through selective pressure on the ibex.

Seasonality and plant defenses

We predicted that seasonality would change the effectiveness of plant defenses. Due to unexpected changes in the availability of different brands of commercial pellets, three different kinds of pellets were used during the course of the experiment, and these varied by season. Two simple experiments showed that the ibex significantly preferred the Harlan pellets used in summer to the Altromin pellets used in fall and winter. This means that some of the differences in GUDs between summer and the following two seasons can be explained by the differences in pellet preferences, reducing some of the explanatory power of the statistical analysis. There were no significant differences in ibex preference between the Koffolk pellets used in spring and either of the other brands.

The results found suggest a mitigating effect of season on effectiveness of mechanical defenses (Figure 2). In summer, fall, and winter, the GUDs of thorn-treated patches were the same as those from control patches, whereas in spring GUDs increased in thorn-treated patches compared to control patches. Although thorns increased handling time and risk of injury, the marginal value of energy was highest in summer, which led to the occurrence of the lowest GUD levels during this season. However, this effect could partially be explained by ibex preference for Harlan pellets used in this season. In other seasons, the marginal value of energy was lower so the foraging costs were higher for ibex and GUDs, therefore, increased in the presence of thorns. The thorn findings suggest that the lowest marginal value of energy occurred in the spring season (highest GUDs.) This may reflect an increase in vegetative growth and abundance post-winter rainfall.

Tannins provided protection to plants during spring, summer, and fall (Figure 3). GUDs from tannin-treated patches were lowest during the summer season compared to others, indicating that ibex increased their intake of artificially provided foods in summer regardless of the presence of tannins. This is similar to the findings of Hakham and Ritte (1993), who showed that ibex increase consumption of alkaloid-producing plants in summer due to

low availability of other foods. GUDs of tannin-treated patches were not significantly greater than non-treated patches in winter. Previous research has shown that the level of condensed tannins increases with leaf maturity in several species of oaks (Makkar et al. 1991) and tropical legumes (Barahona et al. 2003), though similar information could not be found for Negev species. Given that leaf biomass increases due to increased rainfall in winter, ibex may increase the proportion of young leaves that are lower in tannin content in their total food intake. Various leaf browsers such as kudus (*Tragelaphus strepsiceros*; Cooper & Owen-Smith 1985), howler monkeys (*Alouatta palliata*; Glander 1982), and giraffes (*Giraffa camelopardalis*; Furstenburg & van Hoven 1994) have been shown to select foliage for consumption based on minimizing tannin content. Shrader et al. (2012) showed that during the dry season, elephants (*Loxodonta africana*) selected woody species based on the ratio between palatability (digestibility, crude protein, energy, etc.) and tannins. Given a higher availability of young leaves with low tannin content in the natural environment, ibex would have increased GUDs in tannin treatments during the spring. As the seasons progress, however, available leaves become mature over time with accompanying increase in tannin content. Thus, GUDs from tannin-treated trays would decrease over time relative to control trays. The lower than expected rainfall levels observed in winter 2011/2012 could have resulted in a continuation of this trend due to a continued lack of available young foliage and led to the ineffectiveness of tannins in winter.

Similar to tannins, thorns were not effective in winter. However, they were also ineffective in fall and especially in summer. As discussed previously, these results suggest that decreases in overall food availability led to decreased GUDs in thorn-treated trays. There may exist a threshold level of food unavailability, beyond which thorns cease to be effective defenses. If the “young foliage” explanation above is correct, effectiveness of tannins on the other hand seems to change gradually relative to the amount of new leaves available in the environment. The effectiveness of both of the defenses, therefore, are still very much dependent on food availability (quantity and quality) in the environment, which is in turn dependent on rainfall.

Water

Complementarity of food and water

We found that overall there was no significant effect of water availability on GUDs, meaning that ibex GUDs were the same in the presence of water as in the absence of water (Table 1). This result is unexpected and did not support the prediction of complementarity between food and water. We found that water and season interacted significantly to affect GUDs (Table 1), with water increasing GUDs in the hot, dry summer, but not in the other seasons (Figure 5). This contrasts with the results of Hochman and Kotler (2006a) where added water in the early fall (October) resulted in a decrease in ibex GUDs demonstrating a complementarity of food and water. Molokwu et al.

(2010), found that during seasons of low water availability and moderate food abundance, water augmentation improves the quality of the surrounding environment as well as the quality of the patch. If food and water are complementary for ibex, one possible explanation of these surprising results is that the added water may have allowed ibex to exploit more of the dry vegetation in the surrounding area, effectively rendering the environment richer. Therefore, ibex may have chosen to eat more of the foods available in the environment rather than the pellets in the trays resulting in increased GUDs on water-augmentation days. In summer, when water is at lowest availability, this effect should be the strongest, but in wetter seasons the effect would be less strong, hence the lack of significance in the other seasons. As these results are inconclusive, more research is needed to understand the effect of water on environmental quality as opposed to artificial patch quality.

Effect of water on tannins

There was no significant interaction between tannins and water suggesting that water does not mitigate the effect of tannins. Similar results have been found in the literature. Shrader et al. (2008) found that water did not mitigate the effect of tannins for South African goats. These results therefore also suggest that water is not able to decrease the inhibition of protein digestion by tannins through dilution.

We predicted that the mitigation of tannins by water would be manifested by a seasonal interaction based on fluctuating rainfall levels. Tannins would have a larger effect in seasons of low water availability and vice versa. The analysis showed that GUDs in tannin-treated patches were greater than control patches during spring, summer and fall, but there was no significant difference in GUDs during winter (Figure 3), suggesting a mitigating effect of water. However, the seasonal rainfall data suggest that there was only a small difference in available water between winter 2011/2012 and spring 2011 (Table 2). In this case, spring and winter months should have had similar differences in GUDs between tannin-treated and control patches. Since this was not the case, the results fail to convincingly show that water has a mitigating effect on tannins.

Implications for herbivory

This research focuses on herbivory from the point-of-view of the optimal foraging strategy of the ibex. Due to the nature of the evolutionary consumer-resource game between ibex and the plants making up their diet, a few conclusions can also be drawn from the point of view of the optimal defensive strategy of the plant. The finding that tannins and thorns are substitutable defenses – in other words that their effects together are merely additive – suggests that in principle, plants could invest in a single defense only and should choose that defense which is less costly to produce. However, it was also found that tannins were effective in summer whereas thorns were not, suggesting that plants should invest in the use of tannins in summer regardless of their cost relative to the cost of

thorn production. The “young foliage” explanation for increased GUDs in tannin-treated trays in winter suggests that plants that have relatively high levels of tannins in young leaves would have an advantage over others during summer. Seasonal rainfall promotes growth of new foliage, but also comes with increased ibex attention to new foliage. From the literature, increased levels of browsing can induce increased levels of tannin production in several acacia species (Du Toit et al. 1990; Furstenburg & van Hoven 1994; Rohner & Ward 1997), a response that would seem to have strong adaptive benefits in the light of this experiment. Finally, plants need to defend themselves against multiple herbivore species. Selection pressures are not only the result of ibex preferences, but also those of other herbivores who, unlike the ibex, may not treat thorns and tannins as substitutable defenses. Combining the results of similar comparative research on other Negev herbivores could provide greater understanding of optimal defensive strategies for plants.

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ORCID

Elsita M. Kiekeley  <http://orcid.org/0000-0001-7517-5778>

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