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Diet selection by domestic and wild herbivore species in a coastal Mediterranean wetland

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Knowledge of the diet selection by coexisting herbivores is of prime importance in order to draw guidelines for livestock management alongside wildlife conservation. In this study, diet selection by coexisting cattle (*Bos taurus*), feral horses (*Equus caballus*), European hares (*Lepus europaeus*) and white-fronted geese (*Anser albifrons*) was evaluated in coastal grazing lands of the Evros Delta, Greece. Graminoids constituted the primary forage category for all herbivores, since they contributed more than half in the herbivores' diets. Even though legumes and forbs constituted a substantial part of their diets, selection indices of these forage categories did not exceed the value of 1, which indicates significant selection. Halophytes were selected by all herbivores to a much smaller degree than expected in view of their availability. Increasing the abundance, primarily of graminoids and secondarily of legumes and forbs, is expected to benefit all the studied herbivores.

Introduction

Wetlands are sensitive ecosystems inhabited by numerous mammalian and avian herbivore species. These ecosystems provide many products and services which contribute both to the welfare and health of humans (Tsiouris & Gerakis 1991). However, wetlands are among the most degraded ecosystems mainly due to inappropriate management and other human interventions (Amezaga *et al*. 2002). One of the most important uses of wetlands is the grazing by livestock and wild herbivores (Berg *et al*. 1997, Loucougaray *et al*. 2004). The selected forage categories by coexisting herbivores is a prerequisite for understanding livestock–wildlife interactions, their impact on the vegetation communities (Persson *et al*. 2000, Suominen & Olofsson 2000, Suominen *et al*. 2008), as well as to predict their patch choice and spatial distribution (Ball *et al*. 2000, van der Graaf *et al*. 2007, Kuijper & Bakker 2008).

The Evros Delta in Greece is a wetland with high biodiversity, since more than 300 bird species, including many protected and globally threatened species use this area, either for specific periods or all year round (Goutner 1997). Coastal grazing lands of the Evros Delta serve primarily as feeding and resting areas for several mammalian and avian herbivores. The major herbivore assemblages in this area are cattle (*Bos taurus*), feral horses (*Equus caballus*), European hares (*Lepus europaeus*, hereafter hare) and

Fig. 1. Location of the study area (indicated with an arrow).

white-fronted geese (*Anser albifrons*, hereafter geese). According to the concept of hierarchical foraging, herbivores select their food on several scales, from landscape down to individual bite level (Bailey *et al*. 1996). Hares and geese are likely to be more selective than cattle at a fine scale. Since geese and hares have smaller bodies and mouths than cattle and horses, it is expected that they have a greater ability to feed selectively on plant species as well as on certain parts of the plants (Illius & Gordon 1992, Perry & Pianka 1997). In comparison to hind-gut fermentors, ruminants are better able to use broadleaved plant species (especially legumes), which usually contain higher amounts of secondary compounds in relation to graminoids (Krysl *et al*. 1984). On the other hand, hind-gut fermentors are better able to make use of short vegetation due to their mouth morphology and dental anatomy than large ruminants (Gordon 1989, Putman *et al*. 1991). Comparisons between feral horses and cattle have shown that the former may consume foods higher in fiber due to the faster rate of food passage through their gut (Olsen & Hansen 1977, Duncan *et al*. 1990). Consequently, in cases of food limitations, it would be expected that equids fair better than cattle in grass-dominated habitats (Menard *et al*. 2002).

There is evidence that livestock and wild herbivores use rather grass-legume-forb patches than halophytic vegetation in the coastal grazing lands of the Evros Delta (Karmiris *et al*. 2008). However, it is unclear if this behaviour origins from their predilection to feed selectively on the available forage in the former patches, i.e. on graminoids, legumes and forbs. The aim of this study was to investigate the diet selection (the basic forage categories) by coexisting cattle, feral horses, hares and geese in coastal grazing lands of the Evros Delta, Greece, during the critical winter period. The null hypothesis tested in this study, that there is no significant selection on the available forage categories by domestic and wild herbivores should be false at least for some forage categories. Diet selection of coexisting herbivores will likely contribute to a better understanding of their forage needs and the potential interactions among them, as well as may help to predict their impact on forage categories and their role in ecosystem processes. Indubitably, such knowledge is valuable in drawing up guidelines for rational livestock management and wildlife conservation in the Mediterranean wetlands.

Methods

Study area

The study was conducted in an unfenced area (Fig. 1) of about 1500 ha along the coastal grazing lands of the Evros Delta, Greece (40°47´N, 26°03´E). About 20% of this area was covered by water during the study. The climate is typical Mediterranean with cold winters and hot dry summers. The mean annual rainfall and temperature are 554.0 mm and 15.0 °C, respectively. During the winter period, cattle (about 1500 cows) grazed freely throughout the study area and over winter their diet was supplemented with roughages and grains. Supplements were provided *ad libitum* at several sites in the study area. This area is commonly shared by the four herbivores and it constitutes the main feeding place for them during the winter period. During the rest of the year, this area is still utilized by the mammalian herbivores (cattle, horses and hares) but their feeding range usually expands to other parts of the Evros Delta as well, while geese habitually fly from the Evros Delta in early to mid-March to their breeding areas in northern Europe (Kazantzidis & Noidou 2008). The feral horses consisted of approximately 30 individuals during the winter season of 2006–2007 and 2007–2008. The mean number (± SD) of the geese in the study area (during the winter of 2006–2007) was 821 ± 64 individuals (Kazantzidis & Noidou 2008), whereas the density of hares, as inferred by the accumulation rate of pellets, was about one individual per 15 ha (Karmiris *et al*. 2008). Also in the area, there are certain other avian herbivores whose numbers however, are relatively low and fluctuate, such as 41–54 individuals (from October to early March) of the globally threatened lesser white-fronted goose *Anser erythropus* (Panagiotopoulou *et al*. 2009); occasionally the red-breasted goose *Branta ruficollis*; and a few species of the Anatidae family (Kazantzidis & Noidou 2008).

Since 1986, the study area has been protected under the Ramsar convention as a wetland of international importance (Ministry of Environment 1986); it is a part of the Natura 2000 network and it is also a Special Protection Area. Several human activities, such as hunting, agriculture, livestock farming, fishing and recreation, are carried out in this wetland. Over the last 60 years, various draining projects were instigated, whose primary objective was to increase the amount of arable land, such as the alignment of the lower route of the Evros River (Angelidis & Athanasiadis 1995). As a result, a decrease in the fresh water level horizon and the concomitant increase of soil salinity was observed in the study area. It was inevitable that such environmental conditions would benefit the dominance of halophytes over other plant species, sensitive to salinity. As a result, the vegetation communities in the study area are both variable and patchy due to the shifting properties of the environmental conditions, namely, the presence or absence of water, its quality, depth, levels of salinity, etc. There is no arable farmland in the study area, but farming occurs in the vicinity (to the north of the study area). The most important crops are cereals (mainly wheat), followed by sugar beet, corn, cotton, etc.

Availability of major forage categories

Two major habitat types in a patchily mosaic form, i.e. halophytic and grass–legume–forb patches (Table 1) are distinguished based on the dominant plant species in the study area (Karmiris *et al*. 2008). Halophytic vegetation cover was about twofold higher than all the other forage categories together. This mosaic is highly dynamic in time, depending primarily on how frequently seawater flows into the study sites. Woody species (mainly *Tamarix* spp.) occur solitary or in a few small groups, mainly in halophytic patches throughout the study area. Their participation in the vegetation composition was less than 1.5% in the study area during the years 2006–2008 (Papachristou *et al*. 2008).

Table 1. Habitat types, dominant plant species and vegetation composition in the study area (from Karmiris *et al.* 2008).

Habitat type	Dominant species	Vegetation composition (%)*	
		Halophytes	Graminoids Legumes, Forbs
Halophytic vegetation	*Salicornia* spp., *Limonium* spp., *Halimione portulacoides, Salsola* spp., *Halocnenum strobilaceum*	> 60	< 20
Grassland	*Cynodon dactylon*, *Puccinelia maritima*, *Elymus* spp., *Poa* spp., *Lolium perenne*, *Agropyron* spp., *Carex* spp., *Taraxacum officinale*, *Plantago* spp., *Potentilla* spp., *Trifolium* spp., *Medicago* spp., *Artemisia campestris*	> 60	< 20

* Woody vegetation (mainly *Tamarix* spp.) occurs solitary or in a few small groups in very low proportions (less than 1.5% of the vegetation composition), unable to constitute a distinct habitat type.

The availability of the major forage categories for all herbivores was based on the relative cover of vegetation in the study area. Vegetation cover was assessed in 150 plots (1 m^2), randomly dispersed throughout the study area (Cook & Stubbendieck 1986). In order to objectively estimate the vegetation cover, visual estimates were made for each forage category using a 10 × 10 cm grid (i.e. each grid equaled 1% cover when used on 1 m^2 plots). Data were collected during four vegetation inventories in the early (November–December) and the late (January–February) winter in two consecutive years (2006–2007 and 2007–2008). In total, 16 inventories (2 years × 2 periods × 4 inventories) were carried out during the study. The availability of each major forage category was estimated by excluding litter, bare soil and water proportions. Woody vegetation was also excluded, since this forage category was a negligible component in both the plant community and the herbivores' diet (Markkola *et al*. 2003).

Diet estimation

Fresh faecal subsamples from cattle, feral horses, hares and geese (Bang & Dahlstrøm 2004) were collected at the same time as the vegetation inventories. Approximately 400 fresh droppings from geese and hares were collected in each inventory. In the cases where a pile of droppings was found, only one to two droppings were collected. Fresh faecal material was collected from 200 dung of cattle and horses in each inventory. During collection, an equal quantity of table salt (NaCl) was mixed with the faecal material to avoid decomposition (Litvaitis *et al*. 1996).

Sixteen composite samples of faeces were prepared and analyzed for each herbivore species and inventory. The faecal samples were oven-dried at 105 °C for 24 hours and then ground through a 1-mm screen. Each ground sample was mixed thoroughly to ensure particle uniformity. Five slides were prepared per composite sample. Twenty systematic fields per slide were examined for particle frequency. A field was considered to be the area delineated by a microscope using 100× magnification. Diet composition was determined by microscopic analysis of a composite sample for all herbivore species at 100× and in some cases 200× magnification (Litvaitis *et al*. 1996), using the frequency addition procedure, i.e. dividing the frequency of each category by the total number of frequencies for all categories (Holechek & Gross 1982). Hairs and trichomes were disregarded (unless they were attached to identified epidermal tissue). On average, 368 particles per slide (range 337–414) were identified in the herbivores' faeces in all cases.

Differential digestibility of forage groups may bias potential estimates of herbivore diets, particularly when shrubs or forbs are a major component of the diet (Gill *et al*. 1983, Leslie *et al*. 1983). In such cases it may be more appropriate to calculate correction factors for each of the ingested forage categories (Vavra & Holecheck 1980, Leslie *et al*. 1983, McInnis *et al*. 1983). However, correction factors can be affected by local conditions (Bartolomé *et al*. 1995) and their usefulness is questioned in several studies (Alipayo *et al*. 1992, Cuartas & García-González 1996, Paola *et al*. 2005). Historically, it is well documented that a microhistological analysis of faeces provides an accurate and precise method to estimate diet composition of herbivores without calculating correction factors (Holechek & Gross 1982, Alipayo 1991, Paola *et al*. 2005), especially in grazers (Alipayo *et al*. 1992, Bartolomé *et al*. 1995, Shrestha & Wegge 2006).

The most common plant species present in the study area (74 species) were collected and microscope slides were prepared of identified reference plants for comparative purposes. Special attention was paid to collecting several plant parts (stems, flowers, fruits, stolons, etc.) when these were available in the study area during the winter period.

Selection of major forage categories

Each plant species identified in the herbivores' faeces was assigned to one of the following forage classes: (1) halophytes, (2) graminoids, (3) non-leguminous forbs (hereafter forbs), (4) legumes, and (5) woody vegetation. Selection indices ($\hat{w}_i$) for graminoids, legumes, forbs and halophytes (woody vegetation was excluded) were calculated as:

$$\hat{w}_i = \frac{o_i}{p_i} \quad (1)$$

where o_i is the proportion of used resource units and p_i is the proportion of available resource units. The standardized selection index Bi (Krebs 1999) was also calculated according the formula:

$$\mathrm{Bi} = \frac{\hat{w}_i}{\sum_{i=1}^{n} \hat{w}_i} \quad (2)$$

where, Bi is the standardized selection index for species i, and $\hat{w}_i$ is the selection index for species i. Standardized selection indices for all forage resources add up to 1 and in essence give the probability of selection of forage resource i in case of equal availability of all resource categories.

Data analysis

We tested the null hypothesis of no selection using the *G*-test (Krebs 1999):

$$\chi^2 = 2\sum_{i=1}^{n}\left[u_i \ln\left(\frac{u_i}{Up_i}\right) + m_i \ln\left(\frac{m_i}{m_i + u_i \dfrac{M}{U+M}}\right)\right] \quad (3)$$

where χ^2 is the Chi-squared value with $n - 1$ degrees of freedom, u_i is the number of observations using resource i, m_i is the number of observations of available resource i, U is the total number of observations of use (i.e. Σu_i), M is the total number of observations of availability (i.e. Σm_i) and n is the number of resource categories.

Standard errors of selection indices were calculated using the formula:

$$s_{\mathrm{wi}} = \sqrt{\frac{(1-o_i)}{Uo_i} + \frac{(1-p_i)}{p_i M}} \quad (4)$$

where s_{wi} is the standard error for a selection index and the other terms as defined above. 95% confidence intervals (CI) for selection indices were calculated using the Bonferroni correction as:

$$\hat{w}_i \pm z_{0.0125} s_{\mathrm{wi}} \quad (5)$$

Confidence intervals of selection indices not containing the value of 1 indicate significant selection. If a confidence interval contains the value of 1 then the selection index does not differ from that value at $\alpha = 0.05$, i.e. there is no selection for or against the forage category.

Results

Forage availability

Halophytes were the dominant available forage category since they constituted almost 57% of the total available food categories in the study area. Graminoids were the second most available forage category to herbivores (22.9%), followed by forbs (13.1%) and legumes (7.1%).

Selection of major forage categories

Selection indices had similar trends both between years (2006–2007 and 2007–2008) and periods (early and late winter) and their 95% confidence intervals highly overlapped; these data are thus reported here as a whole. The major forage category for all herbivores was graminoids (Table 2). This forage category comprised over 50% of the winter diets of all herbivores. Selection indices of graminoids exceeded by far the value of 1 (Table 3), which indicates that graminoids were preferentially selected. Among this forage category, the grass species *Lolium perenne*, *Cynodon dactylon*, *Puccinelia maritima*, *Poa* spp., *Elymus* spp., *Agropyron* spp., etc. were consumed more often by all four herbivores.

Legumes and forbs were also important forage categories for the herbivores in the study, especially for the cattle. More specifically, cattle consumed more legumes (7.0%) than the other three herbivores and the selection index did not differ significantly from 1. Conversely, hares consumed higher percentages of forbs, most of which belonged to species of the *Compositae* and *Cruciferae* families, than the other herbivores. Selection indices of legumes were higher than of forbs, except in the case of hares. Various species of legumes and forbs were identified in the faeces of all herbivores; these included *Trifolium* spp., *Medicago* spp., *Taraxacum officinale*, *Plantago* spp., *Potentilla* spp., *Artemisia* *campestris*, etc. The majority of the legumes consumed by geese belonged to the *Trifolium* species (mainly *T. repens* and *T. subterraneum*).

Halophytes were also consumed by all herbivores studied; however, selection indices of halophytes were the lowest as compared with those of the other forage categories. The most important species, which were consumed by all herbivores, were *Halimione portulacoides*, *Salicornia* spp., *Salsola* spp. and *Limonium* spp. The proportion of halophytes was about twofold higher in the diets of the large herbivores (cattle and feral horses) than in the medium-sized ones (hares and geese), but in all cases halophytic consumption was far less than their availability in the study area.

An important constituent of the cattle's diet was the seeds and green matter of *Vicia sativa*, which was given by livestock raisers as a supplement. Obviously, the available forage for cattle is inadequate during the winter period and raisers need to provide extra food to livestock. However, supplementary food was also detected in the faeces of the other herbivores being studied, which means that feral horses, hares and geese came across the remains of the supplementary fodder within the study area but managed to consume only a small amount since the total percentage of supplements in their diet composition was negligible (traces).

Cereal crops (primarily wheat) lay outside the study area and were consumed in notable amounts mainly by geese (9.9%) and secondarily by hares (6.0%). Woody vegetation was only rarely consumed by the three mammals, while it was not found in the faeces of the geese. The low

Table 2. Diet composition (%) for major forage categories of cattle, feral horses, hares and geese in the coastal grazing lands of the Evros Delta, Greece during the wintering periods (November to March) of two consecutive years (2006–2007 and 2007–2008). Figures are based on 16 samples of faeces for each herbivore. tr = traces (less than 1%), – = not found.

Forage resource	Cattle	Feral horses	Hares	Geese
Halophytes	16.2	15.1	8.8	8.7
Graminoids	54.6	66.5	63.9	61.1
Legumes	7.0	5.4	5.1	5.1
Forbs	4.6	4.9	10.2	4.3
Woody vegetation	tr	tr	tr	–
Supplementary food	9.4	1.4	tr	tr
Cereal crops	–	–	6.0	9.9
Animal matter	–	–	–	1.8
Unidentified	7.9	6.5	4.5	8.4

Table 3. Selection indices ($\hat{w}_i$ ± 95% confidence intervals) and standardized selection indices (Bi) of major forage categories for cattle, feral horses, hares and geese in the coastal grazing lands of the Evros Delta, Greece during the wintering periods (November to March) of two consecutive years (2006–2007 and 2007–2008). Figures are based on 16 samples of faeces for each herbivore and 150 vegetation plots (1 m^2).

Forage resource	Cattle		Feral horses		Hares		Geese	
	$\hat{w}_i$ (95% CI)	Bi	$\hat{w}_i$ (95% CI)	Bi	$\hat{w}_i$ (95% CI)	Bi	$\hat{w}_i$ (95% CI)	Bi
Halophytes	0.284 (0.269–0.300)	0.071	0.265 (0.249–0.281)	0.062	0.154 (0.134–0.175)	0.035	0.153 (0.132–0.173)	0.039
Graminoids	2.382 (2.365–2.400)	0.595	2.901 (2.884–2.919)	0.673	2.788 (2.771–2.805)	0.627	2.666 (2.648–2.683)	0.682
Legumes	0.994 (0.955–1.033)	0.088	0.767 (0.725–0.809)	0.087	0.724 (0.683–0.766)	0.176	0.724 (0.682–0.766)	0.084
Forbs	0.352 (0.317–0.388)	0.248	0.375 (0.340–0.411)	0.178	0.781 (0.752–0.810)	0.163	0.329 (0.293–0.366)	0.185

consumption rates indicate that it did not constitute an important food source for the herbivores in our case study.

Discussion

Graminoids constituted the main food for the herbivores of the Evros Delta, as in many other studies in European coastal grazing lands (Ortega *et al*. 1997, Vickery & Gill 1999, van der Wal *et al*. 2000, Menard *et al*. 2002). This category, however, represents only a part (22.9%) of the available forage categories in the study area which is dominated by halophytic biomass (57.0%). Given this particular condition (namely the halophytic dominance), it seems that selection of the graminoids by grazing livestock and wildlife may have the effect of suppressing their abundance in this area. Indisputably, this may cause structural changes in vegetation communities in the study area and may further distort the equilibrium of the ecosystem, an equilibrium which is already threatened by several human activities. Under this perspective, conservational strategies should focus on the protection of graminoids from overgrazing.

Legumes and forbs are also considered important forage categories, at least for cattle (Krysl *et al*. 1984, Menard *et al*. 2002), hares (Karmiris & Nastis 2010) and geese (Vickery & Gill 1999). Surprisingly, in this study, the only forage category which was preferentially selected by all herbivores was graminoids, while legumes and forbs were consumed less than it was expected in view of their availability. This is an exception to the general theoretical approach that morphological and physiological differences among herbivores should result in diet selection differences too (Hofmann 1989). This outcome (non preferentially selection for legumes and forbs) further aggravates the potential consequences of heavy grazing pressure on graminoids, in case of imbalance between availability of graminoids and the number of herbivores in the coastal grazing lands of the Evros Delta. Nevertheless, selection indices of legumes for cattle were close enough to the threshold of preferentially selection, which indicates that this forage category might also play a role in the decision of movements and the spatial distribution of cattle in the study area.

In order to minimize potential competitive interactions for food and habitat and to ensure coexistence among herbivores in the Evros Deltra, conservational approaches should focus on the reduction of the halophytic dominance. From this perspective, a higher carrying capacity can be achieved in this area (van der Wal *et al*. 2000). Nevertheless, halophytes despite their insubstantial value as forage for herbivores, might provide cover which could be of particular importance to vulnerable species, such as hares and geese. At the moment, the role of halophytes in the ecology of hares and geese still remains unclear. Hence, the investigation of the role of the halophytic community in wildlife ecology will contribute to the sustainable multiple use of coastal grazing lands of the Evros Delta.

Cereal crops may constitute a substantial part of the diets of geese and hares (Frylestam 1986, Chapuis 1990, Vickery & Gill 1999) and may attract wild herbivores outside of the protected (non hunting) area (Bos *et al*. 2005a, Fox *et al*. 2005). However, in our study the consumption of winter cereals by these herbivores was relatively low. The relatively limited availability of graminoids in our study area may be a critical factor in explaining the use of cereal crops by both geese and hares. On the other hand, concern for economic damage caused by these herbivores to cereal crops is considered negligible in the winter months as the crops are in an early phase of development. At this stage, the plant, unless uprooted, is usually able to compensate for most of the damage incurred (Kear 1970, Wallin & Milberg 1995).

Management implications and future research

Increasing the availability of graminoids in the Evros Delta (e.g. by seeding), until an upper limit is reached, will probably benefit all the herbivores studied, since this will increase the availability of their selected food. In this system however, increasing the availability of graminoids inevitably means that halophytic cover will be reduced lessening its potential protective role as a shield against predators. Hence, such approaches should be monitored in long term, since altering the relative cover of the different vegetation types may have unforeseeable consequences in the ecosystem. As the movements of all herbivores in this area are influenced by the presence of grass–legume–forb patches (Karmiris *et al*. 2008), a more even distribution of these patches throughout the study area is expected to maximize the area that these herbivores use. When forage availability is limited, as probably happens in years with high numbers of wild herbivores, cattle stocking rates should be kept at a relatively low level and livestock raisers should provide increased quantities of supplementary food dispersed throughout the study area.

Several studies have shown that livestock (cattle, sheep, goat) grazing benefits species of lagomorphs and anseriformes on the northwestern European coast, by retarding vegetation succession and maintaining a low vegetation height (Huisman & Olff 1998, van der Graaf *et al*. 2002, Bos *et al*. 2005b, Bakker *et al*. 2009). Hares along with geese and other waterfowl have also been recorded to use the grass–legume–forb patches with a low vegetation height more than the halophytic ones with much taller vegetation in the Evros Delta (Karmiris *et al*. 2008). As long as forage and habitat resources for domestic and wild herbivores are not depleted, then livestock grazing is a valuable 'tool' in manipulating wildlife habitats (Vickery & Gill 1999, van der Wal *et al*. 2000, Karmiris & Nastis 2007). It would appear that livestock grazing at moderate grazing intensity, i.e. about 50% of the above standing biomass is left ungrazed, is vital for the presence of these medium-sized herbivores in the Evros Delta. Otherwise, the suitability of coastal grazing lands of the Evros Delta as feeding sites for hares and geese would probably be reduced. Future research should focus on the possible interactions among the herbivore assemblages under various grazing regimes in the Evros Delta and how they can be regulated in order to effectively conserve coastal Mediterranean ecosystems.

In cases of high geese numbers, the consumption of cereals by geese is expected to rise and the economic damage to crops may be substantial. A number of solutions are proposed to deal with such cases, e.g. compensation to farmers, culling of geese, restoration of natural habitats etc. However, the most promising and feasible solution is the creation of alternative feeding areas for geese (Owen 1990, Percival 1993, Vickery & Gill 1999). For these reasons geese numbers and movement; availability of natural forage; and diet composition of herbivores in the Evros Delta constitute essential parameters which should be monitored frequently. Management plans need to also be flexible according to shifting conditions. Should this hold, then there will be much less damage to neighboring agricultural crops by wildlife, and coastal grazing lands will be able to support more herbivores per surface unit in a sustainable manner for longer time periods.

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