Avocetta 34: 21-28 (2010)

Variation in diet composition of wintering waterfowl among Greek wetlands

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Abstract – The aim of this study was to determine the diet composition of wintering waterfowl, and assess its variation among Greek wetlands. Digestive tracts (oesophagus, proventriculus and gizzards) of Gadwall *Anas strepera*, Eurasian Wigeon *Anas penelope*, Eurasian Teal *Anas crecca*, Mallard *Anas platyrhynchos*, Northern Shoveler *Anas clypeata*, Northern Pintail *Anas acuta* and Common Coot *Fulica atra* were collected in four Greek wetlands (Evros Delta, Lake Vistonida, Aliakmon-Axios Delta and Messolonghi Lagoon), during two wintering periods from October 2004 to March 2006. Diet composition was evaluated using the percentage of occurrence and the aggregated percent dry weight methods. Gadwall and Wigeon were primarily herbivorous (both more than 95% dry weight), Teal and Mallard mostly relied upon seeds for food (60-75% dry weight), whereas Shoveler, Pintail and Coot consumed elevated quantities of invertebrates (27.4%, 16.8%, and 31.2% dry weight respectively). *Scirpus* consumption by Teal and Mallard was lower in Messolonghi Lagoon than in the other wetlands. Conversely, increased quantities of *Ruppia* spp. and invertebrates were recorded in waterfowl diets (except Teal) in Messolonghi Lagoon. These findings may be attributed to the variation in food availability among study areas, thus management plans should be focused both upon the targeted bird species and the particular wetland separately. In general, since studied species exhibit considerably forage plasticity, providing increased habitat heterogeneity seems to be the best management approach for wintering waterfowl in Greece, at least under their dietary needs' aspect.

Riassunto – Scopo di questo studio è definire la dieta di anatre e folaga svernanti, e inoltre di definirne le variazioni in differenti aree umide greche. Sono stati raccolti esofagi, proventricoli e ventrigli di canapiglia, fischione, alzavola, germano reale, mestolone, codone e folaga in quattro aree umide greche (delta dell'Evros, lago Vistonida, delta dell'Aliakmon-Axios e laguna di Messolonghi), durante due inverni, dall'ottobre 2004 al marzo 2006. La composizione della dieta è stata valutata utilizzando due metodi, la percentuale di occorrenza e la percentuale aggregata sulla sostanza secca (s.s.). Canapiglia e fischione sono prevalentemente erbivori (entrambi >95% della s.s.), alzavola e germano reale dipendono molto dai semi (60-75% della s.s.), mentre mestolone, codone e folaga consumano elevate quantità di invertebrati (rispettivamente 27.4%, 16.8% e 31.2%). L'utilizzo di *Scirpus* da parte di alzavola e germano è risultato minore a Messolonghi rispetto agli altri siti. Al contrario, quantità maggiori di *Ruppia* spp. e di invertebrati sono stati rinvenuti maggiormente (eccetto che per l'alzavola) in questa laguna. Questi risultati possono dipendere a variazioni nella disponibilità di cibo tra aree diverse, per cui i piani di gestione dovrebbero basarsi sia sulle specie obiettivo, sia sulle caratteristiche delle diverse aree. In generale, poiché le specie studiate hanno mostrato una notevole plasticità trofica, una gestione basata sull'incremento dell'eterogeneità ambientale pare la migliore scelta gestionale per anatre e folaga svernanti in Grecia, quantomeno sotto l'aspetto trofico.

INTRODUCTION

The diet composition of waterfowl has been thoroughly investigated in Europe and other areas of the world (McKnight and Hepp 1998, Tamisier and Dehorter 1999, Durant *et al*. 2006). However, there is a lack in knowledge about the diet composition of wintering waterfowl and its variation among Greek wetlands and generally from the eastern Mediterranean region. The majority of waterfowl species winters in Greece and returns for breeding to northern Europe and Russia in late winter to early spring (Handrinos and Akriotis 1997). It is well documented that food plays a major role for these birds in order to withstand the harsh weather conditions during winter and also to be prepared for their trip back to breeding areas (Baldassarre and Bolen 2006). An assessment of foods consumed by wintering waterfowl is basic for understanding their feeding ecology and essential for the appropriateness of their habitat management. Thus, it is of crucial importance to broaden the scientific knowledge about the feeding habits of wintering wildfowl species in Eastern Mediterranean wetlands.

The principal factor influencing the selection of foods by waterfowl and subsequently their diet composition (Sedinger 1997, Nudds *et al*. 2000, Durant *et al*. 2006); as

Received 15 December 2008, accepted in revised form 24 October 2010

well as the use of different wetlands or sites within wetlands (Durant *et al*. 2004, Durant and Fritz 2006, Klaassen *et al*. 2007) is considered to be the availability of foods. The abundance, accessibility and the nutrient content of potential foods may be quite different between Mediterranean wetlands, as a combined result of many environmental factors, such as the level of salinity, the water depth and turbidity, the light and temperature, the nutrient level of the waterbody (Verhoeven 1979, Bonis *et al*. 1995, Bonis and Grillas 2002, Taft *et al*. 2002). However, waterfowl are considered to be flexible species able to adjust their foraging strategy to many temporal and space variant factors, such as predation, hunting pressure and techniques, protection from adverse weather conditions, human disturbance (Pöysä 1987, Guillemain *et al*. 2002a, 2002b, Paillisson *et al*. 2002). Thus, there is a potential that individuals of the same species may rely upon different food resources in different wetlands in Greece, as it has already been mentioned for wigeon in North-Western Europe (Durant *et al*. 2006).

The aims of the study were: a) to define the wintering diet composition of seven waterfowl species in four coastal Greek wetlands, b) to assess whether consumption of the major food categories differs for each species among wetlands, and c) to integrate these results in order to direct wetland management for the benefit of waterfowl populations. This is a rare study of Mediterranean wintering birds' diet, and probably the first of its kind from the eastern Mediterranean region.

MATERIAL AND METHODS

Study areas

The study was conducted in the Messolonghi Lagoon (38° 20' N, 21° 15' E), Evros Delta (40° 47' N, 26° 03' E), Lake Vistonida (41° 04' N, 25° 11' E) and Aliakmon-Axios Delta (40° 26' N, 22° 38' E) (Fig. 1). These are among the most important wetlands in mainland Greece for wintering waterfowl. Greece, despite its small size, is one of the most important countries in the Eastern Mediterranean-Black Sea region regarding the wintering population of Anatidae and coot (Athanassiou 1987). During the period 1982-1992 the average number of swans, geese, ducks and coots wintering in Greece was 345,000 (Handrinos and Akriotis 1997). In 1995, a percentage of 29.5% of the total wintering Anatidae and coot population in this region was distributed among Greek wetlands, indicating their importance for the wintering waterfowl (Delany *et al*. 1999).

All the study areas are protected under the Ramsar convention and are part of the Natura 2000 network. Several human activities such as hunting, agriculture, livestock farming, fishing and recreation are performed in all of them. Vegetation communities are very variable and

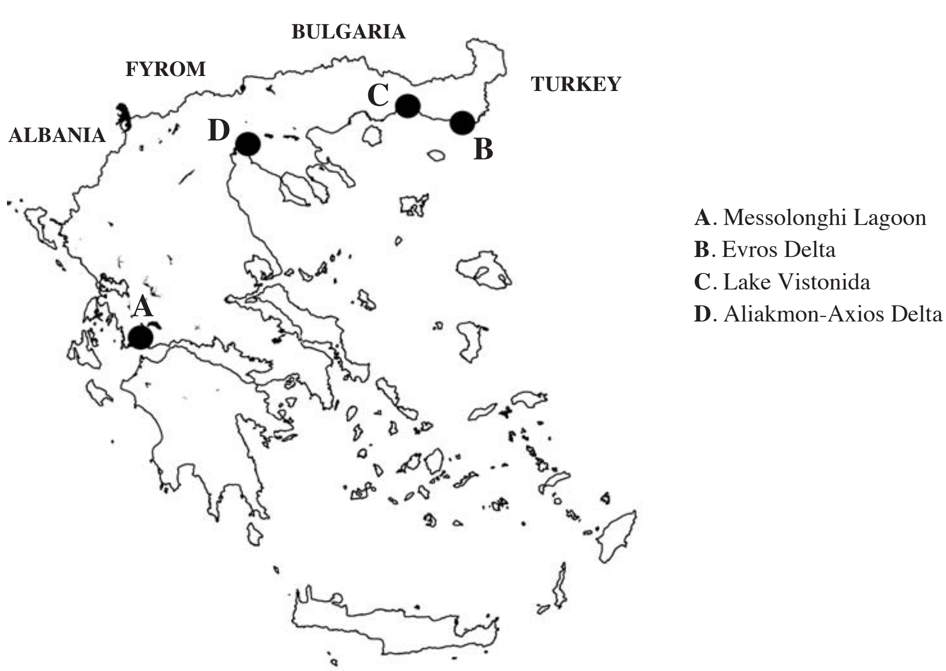

Figure 1. Location of the four study areas in Greece – *Localizzazione delle quattro aree di studio in Grecia*.

patchy in these wetlands due to the dynamic character of environmental conditions; mainly the presence or absence of the water, its quality, depth and salinity level. These conditions are influenced either by natural or artificial causes (seasonal and annual variation of precipitation and temperature, pollution, creation of water barriers, drainage, etc.), resulting in an unstable mosaic of aquatic, halophytic and terrestrial plant communities.

Sample collection, handling and analysis

We collected waterfowl that had been harvested by hunters during the wintering period (October to March) for two consecutive hunting seasons (2004-06). A few of them (N=15) in Evros Delta and Messolonghi Lagoon were shot illegally and confiscated. Digestive tracts (oesophagus, proventriculus and gizzards, N=377) of Gadwall *Anas strepera*, Eurasian Wigeon *Anas penelope*, Eurasian Teal *Anas crecca*, Mallard *Anas platyrhynchos*, Northern Shoveler *Anas clypeata*, Northern Pintail *Anas acuta* and Common Coot *Fulica atra* were removed as soon as possible after harvesting in all study areas. Samples were collected in the morning and in the afternoon, thus the food samples should be representative of what birds consumed both on their feeding grounds and on day-roosts (Guillemain and Fritz 2002). Each sample was numbered and labeled to species, sex, age group (adult-immature using plumage characteristics), site, and date. The majority of samples were preserved in 80% ethyl alcohol, while a few of them were deep frozen (-18 ^{o}C) after harvesting. Food items found in oesophagus, proventriculus and gizzards were dried to a constant mass at 65 ^{o}C for 48 hours and weighed (± 0.0001g). Diet composition was evaluated using the percentage of occurrence (F) and the aggregated percent dry weight methods (DW) (Swanson *et al*. 1974a). Seeds and plant species from aquatic, shoreline and terrestrial sites were gathered to serve as a reference collection. Plant matter was identified to the genus and frequently to the species, invertebrates to the order and some to the family or to the genus (Campredon *et al*. 1982, Legagneux *et al*. 2007). Empty digestive tracts or those which contained either fewer than 5 food items or less than 0.05 g of food were excluded from subsequent analysis (Woodin and Swanson 1989, Petrie and Rogers 1996). In total, 280 digestive tracts were analyzed in both years (Tab. 1).

Statistical analysis

For comparisons among the four study areas, food items were combined into the following three categories: *Scirpus* spp. (seeds), *Ruppia* spp. (seeds and green parts) and total animals. These categories comprised the bulk of the diet composition of all bird species. Two periods were designated, the first included all samples that were collected from October to December, and the second one those from January to March. Mann-Whitney U-tests were used to evaluate differences in diet composition for each bird species between sexes, periods and years. Significant differences in diet composition between wetlands for each waterfowl species were evaluated with Kruskal-Wallis one-way ANOVA (Siegel and Castellan 1988). Further differences between wetlands were evaluated using Bonferroni corrected Mann-Whitney U-tests (Petrie and Watson 1999). In all cases, statistical tests were two-tailed (α= 0.05).

RESULTS

Diet composition

Gadwall consumed plant matter exclusively (Tab. 2). Dry

Table 1. Number of analyzed digestive tracts (combined oesophagus, proventriculus and gizzards) per species collected in four Greek wetlands during the 2004-05 and 2005-06 wintering periods – *Numero di organi dell'apparato digerente (esofagi, proventricoli e ventrigli combinati), per specie, raccolti in quattro aree umide greche durante gli inverni 2004-05 e 2005-06.*

Species	Messolonghi Lagoon	Evros Delta	Lake Vistonida	Aliakmon-Axios Delta	2004-05	2005-06	Total
Gadwall	0*	5	7	1*	3	10	13
Wigeon	7	18	11	4	7	33	40
Teal	65	4	7	15	13	78	91
Mallard	30	6	22	9	14	53	67
Shoveler	5	9	7	1*	4	18	22
Pintail	8	9	0*	1*	7	11	18
Coot	27	0*	1*	1*	7	22	29
Total	**142**	**51**	**55**	**32**	**55**	**225**	**280**

Marked values (*) represent not statistically treated samples

Table 2. Wintering diet composition (combined oesophagus, proventriculus and gizzard) of seven wintering waterfowl species in coastal wetlands of Greece during the 2004-05 and 2005-06 wintering periods – *Composizione della dieta invernale (esofagi, proventricoli e ventrigli combinati) di sei specie di anatre e della folaga nelle zone umide costiere greche durante gli inverni 2004-05 e 2005-06*.

Foods	**Gadwall**		**Wigeon**		**Teal**		**Mallard**		**Shoveler**		**Pintail**		**Coot**	
	DW[a] (%)	**F** (%)	**DW** (%)	**F** (%)	**DW** (%)	**F** (%)	**DW** (%)	**F** (%)	**DW** (%)	**F** (%)	**DW** (%)	**F** (%)	**DW** (%)	**F** (%)
Seeds-Oospores														
Scirpus maritimus	24.0	61.5	8.9	47.5	17.5	57.1	13.5	46.3	26.7	68.2	22.0	50.0	1.8	17.2
Scirpus lacustris	6.7	23.1	0.8	12.5	6.9	38.5	1.0	10.4	3.4	40.9	1.9	27.8		
Other Scirpus	7.9	23.1	1.5	12.5	17.0	48.4	2.8	13.4	4.7	36.4	2.5	22.2		
Ruppia maritima	2.1	30.8	1.4	20.0	15.1	57.1	10.8	41.8	3.0	22.7	11.2	27.8	1.5	20.7
Ruppia cirrhosa			0.5	12.5	5.4	33.0	10.7	29.9	5.0	13.6	3.5	11.1	0.4	6.9
Chara spp.	2.7	23.1	2.3	15.0	3.2	9.9	6.6	19.4	7.0	27.3	6.6	22.2	1.0	10.3
Potamogeton pectinatus			tr	5.0			0.2	9.0						
Najas marina					0.4	2.2	tr	1.5						
Polygonum spp.					0.2	3.3	tr	4.5						
Carex spp.	0.3	7.7			4.7	19.8	1.7	7.5	0.8	4.5	1.9	16.7		
Oryza sativa			2.5	2.5	1.5	5.5	8.8	13.4			6.1	11.1		
Zea mays	2.2	15.4											tr	3.4
Echinochloa crus - galli							0.8	6.0	0.2	27.3	tr	5.6		
Salsola spp.			8.5	25.0	0.1	2.2	2.8	13.4			1.5	5.6		
Suaeda spp.			0.2	2.5	0.3	4.4	0.5	3.0						
Agropyron sp.					tr	1.1								
Puccinelia maritima	1.0	7.7	0.6	10.0										
Unidentified seeds	1.1	15.4	0.9	15.0	2.2	12.1	1.1	10.4	0.6	4.5	1.7	16.7		
Other plant biomass[b]														
Ruppia spp.[c]			6.8	25.0	11.2	35.2	4.4	23.9	1.8	13.6	2.8	11.1	28.4	72.4
Zostera spp.	14.5	30.8	11.9	35.0	1.5	8.8	3.4	11.9	3.3	18.2	3.3	16.7	12.3	37.9
Salicornia spp.	9.9	30.8	11.6	32.5	1.3	6.6	4.1	16.4	6.1	27.3	4.4	22.2		
Halimione portulacoides			2.2	15.0			1.3	4.5	1.9	9.1	2.1	16.7		
Salsola spp.													1.5	6.9
Grasses	9.2	53.8	9.0	32.5			0.5	1.5					6.7	24.1
Potamogeton pectinatus			1.7	20.0	1.0	2.2	4.3	29.9			1.6	5.6	0.7	6.9
Ulva lactuca	3.1	30.8	7.8	30.0	0.1	3.3	1.0	7.5					1.1	6.9
Enteromorpha spp.	2.3	23.1	4.0	22.5	0.4	3.3	0.7	6.0					2.3	6.9
Ceratophyllum spp.			2.0	15.0										
Lemna spp.	1.8	23.1					0.5	6.0					0.9	6.9
Unidentified	11.2	69.2	12.2	65.0	6.7	49.5	9.9	56.7	8.1	68.2	10.2	61.1	10.4	62.1
Total plant	**100**		**97.4**		**96.9**		**91.4**		**72.6**		**83.2**		**69.0**	
Animal matter														
Limnaea spp.			0.8	5.0	1.1	8.8	1.8	11.9	10.3	40.9	0.6	22.2	4.9	27.6
Turritellla spp.					0.7	4.4	2.4	9.0			8.0	11.1	8.9	34.5
Planorbis sp.							tr	1.5					1.0	13.8
Other gastropoda			0.9	5.0	1.1	2.2	1.1	6.0	13.9	27.3	7.8	11.1	10.3	48.3
Bivalves			0.7	2.5	tr	1.1	3.1	22.4	2.7	18.2			5.8	31.0
Gammarus sp.					tr	2.2	tr	3.0	0.5	13.6				
Insects			tr	2.5	tr	1.1	tr	1.5			0.3	5.6		
Fishes			tr	2.5							tr	5.6	tr	3.4
Total animal			**2.6**		**3.1**		**8.6**		**27.4**		**16.8**		**31.0**	

[a] **DW**: aggregated percent dry weight, **F**: frequency of occurrence, tr: dry weight less than 0.1%
[b] includes leaves, stems, rhizomes, bulbs, etc.
[c] includes *Ruppia maritima* and *R. cirrhosa* green biomass, which distinction was doubtful in a few samples

weight of green parts and seeds were almost equally important in diet composition (48.0% DW and 52.0% DW respectively). It consumed mainly plant matter of submerged and emergent vegetation (*Scirpus* spp., *Ruppia* spp., *Zostera* spp., *Chara* spp., etc.), whereas terrestrial vegetation (mainly grasses and *Salicornia* spp.) were at a relatively low level percentage.

Wigeon relied heavily upon plants for food, whereas animal matter was consumed occasionally (2.6% DW). It consumed predominantly leaves, rhizomes, stems and other green matter (67.5% DW), whereas seeds constituted a less important food. Terrestrial natural vegetation (*Salicornia* spp., *Halimione portulacoides*, grasses, etc.) was a non-negligible component of the total diet (32.1% DW), but the majority of the total food was provided by aquatic plants (mainly *Scirpus* spp., *Ruppia* spp., *Zostera* spp., *Ulva lactuca*, *Enteromorpha* spp.).

Teal fed predominantly upon seeds (almost 75% DW) provided by sedges and emergent and submerged macrophytes. Seeds belonging to the genera *Scirpus* and *Ruppia* contributed the bulk of the total diet in Greece (62.0% DW). Natural terrestrial vegetation, agricultural crops and animal matter were consumed rarely.

Mallard consumed mainly seeds and secondarily other plant biomass, whereas animal matter was not an important constituent of its diet composition (8.6% DW). *Scirpus* spp. and *Ruppia* spp. were of prime importance as a food resource, together with other aquatic plants, such as *Potamogeton pectinatus*, *Zostera* spp. and *Chara* spp. Agricultural crops (i.e. waste grain of *Oryza sativa* cultivations) were consumed at a relatively low level (8.8% DW). Terrestrial vegetation was of secondary importance as a wintering food. Shoveler was based upon seeds for food, especially *Scirpus* spp. and *Ruppia* spp., and oospores (*Chara* spp.); which constituted the 49.7% DW of the total diet. Other plant matter played a secondary role since it was infrequently consumed. Animal matter (mainly gastropods) consumption was elevated (27.4% DW).

Pintail consumed mainly seeds (primarily *Scirpus* spp. and secondarily *Ruppia* spp.), which together with oospores constituted up to 47.7% DW of the total diet. Other plant and animal matter were of secondary importance (24.3% and 16.8% DW respectively). Aquatic plants provided the majority of the diet, whereas terrestrial vegetation consumption was very low (8% DW).

Coot consumed up to 64.1% DW plant matter other than seeds, mainly green parts of *Ruppia* spp. (28.4% DW) and *Zostera* spp. (12.3% DW), and secondarily grasses (6.7% DW). Seeds and oospores were consumed in very low proportions (< 5.0% DW). Animal matter consumption, mainly gastropods, was relatively higher compared to the studied *Anas* species.

Spatial variation of major food categories

Significant differences were found in *Scirpus* spp. consumption by Teal (Kruskal-Wallis, x^2=20.020, df=3, P<0.001) and Mallard (Kruskal-Wallis, x^2=21.045, df=3, P<0.001) among study areas. The lowest *Scirpus* consumption was observed in Messolonghi Lagoon and the highest in Evros and Aliakmon - Axios Deltas (Tab. 3).

Increased proportions of the genera *Ruppia* in the diet composition of the studied species were recorded in Messolonghi Lagoon (Kruskal-Wallis-Teal: x^2=34.122, df=3, P<0.001, Mallard: x^2=34.291, df=3, P<0.001, Wigeon: x^2=14.806, df=3, P=0.002, Mann-Whitney-Pintail: $U_{8,9}$=16, P=0.024).

Higher proportions of animal consumption was observed in Messolonghi Lagoon in relation to the other study areas (Kruskal-Wallis-Mallard: x^2=17.093, df=3, P=0.001, Wigeon: x^2=14.881, df=3, P=0.002, Shoveler: x^2=6.211, df=2, P=0.045). For all studied species, the consumption of each of the three major food categories

Table 3. Mean percentages (% dry weight) of the genus *Scirpus* and *Ruppia* and animal matter in Teal, Wigeon and Mallard diets (combined oesophagus, proventriculus and gizzard) in each study area during the 2004-05 and 2005-06 wintering periods – *Percentuali medie (% sostanza secca) dei generi* Scirpus *e* Ruppia*, e della componente animale, nella dieta di alzavola, fischione e germano reale (esofagi, proventricoli e ventrigli combinati), in ciascuna delle quattro aree umide studiate, durante gli inverni 2004-05 e 2005-06.*

Areas	**Teal**			**Wigeon**			**Mallard**		
	Scirpus	*Ruppia*	Animal	*Scirpus*	*Ruppia*	Animal	*Scirpus*	*Ruppia*	Animal
A. Messolonghi Lagoon	32.1 ^{d}	42.2 ^{b,c,d}	1.8	8.6	34.8 ^{b,c}	14.8 ^{b}	3.3 ^{b,c}	55.9 ^{b,c,d}	15.7 ^{c,d}
B. Evros Delta	75.8	3.1 a	2.4	10.1	4.7 ^{a}	0.0 ^{a}	24.5 ^{a}	1.4 ^{a}	0.4
C. Vistonida lake	36.9	1.0 a	9.2	14.2	1.0 ^{a}	0.0	32.0 ^{a}	2.1 ^{a}	4.8 ^{a}
D. Aliakmon-Axios Delta	74.8 ^{a}	8.7 ^{a}	6.0	9.4	2.1	0.0	23.1	0.4 ^{a}	0.4 ^{a}

^{a,b,c} and ^{d} connote significant differences (Bonferroni corrected Mann-Whitney tests, P<0.05) from areas A,B,C and D respectively. Presented only bird species with adequate sample size larger than four in each study area.

was not significantly different between sexes, periods and years (P>0.05 in all cases).

DISCUSSION

Although differential digestion among food items, especially planktonic invertebrates, may influence gizzard analysis in waterfowl (Swanson and Bartonek 1970), this method is particularly useful when comparing diet composition between wetland sites and time, especially when gizzard data are combined with oesophagus and proventriculus data (Green and Sánchez 2003, Fuentes *et al*. 2004). The non-significant differences between periods may reflect our highly heterogeneous sample characteristics, especially the mixing of study areas and years. In fact, the collection of samples from various wetlands, as it was the case in the present study, is considered important for evaluating the feeding habits of waterfowl and provides more accurate estimation of their diet composition, since incorporating only one study area may actually confound the final outcome, i.e. may yield a bias in the diet composition of the involved species (Swanson *et al*. 1974b, Miller *et al*. 2000). Aquatic invertebrates usually lose dry mass when stored in ethanol (Howmiller 1972), thus their relative dry weight may be conservative in the present study. However, the relative absence of significant proportions of animal matter contained in the majority of our samples indicates that their handling (preservation in ethanol) had a non important influence on the invertebrates' dry mass in this study.

Gadwall and Wigeon were almost exclusively herbivorous species in our study and in many others in Western Europe during winter (Owen and Thomas 1979, Thomas 1982, Campredon 1984, Blonder and Aronson 1999). The findings of the present study lead us to the conclusion that aquatic plants, grasses and *Salicornia* spp. constituted the major foods of these species in Greek wetlands during the wintering period. Conservation priorities for Gadwall and Wigeon should focus upon the protection and enhancement of aquatic and terrestrial plant populations, in order to ensure their dietary needs throughout the winter. However, terrestrial habitats surrounding Greek wetlands are usually used as grazing sites by livestock. The interactions between waterfowl and livestock in terrestrial habitats have not been studied in detail (Mesleard *et al*. 1995), despite the fact that these studies may reveal valuable solutions on how to manage these habitats for multiple purposes (waterfowl conservation and livestock development) and how to use livestock as a 'tool' for the benefit of waterfowl populations.

Teal and Mallard can be characterized as granivorous species. The dominance of seeds in their diet composition highlights their importance as a wintering food resource for them. This is in agreement with similar studies in Western Europe (Tamisier 1974, Thomas 1982). Teal and Mallard are considered generalist species and their diet composition may vary between places, according mainly to the availability of food and their dietary needs (Tamisier and Dehorter 1999, Guillemain and Fritz 2002, Hughes and Green 2005). The present findings lead us to the conclusion that elevating diversity of seed bearing plant species will contribute to the viability of Teal and Mallard populations wintering in Greece. However, the bulk of their food in our study was provided by aquatic plants either emerged (*Scirpus* spp.) or submerged (*Ruppia* spp.); hence applied management efforts (improvement of water quality, control of water and salinity levels, regulation of sediment deposition and grazing pressure, etc.) must concentrate primarily on these plant communities.

Shoveler, Pintail and Coot were omnivorous since animal matter was an important component of their diet composition. Shoveler and Pintail also consumed high quantities of seeds. Shoveler often consumes elevated amount of invertebrates (Pirot *et al*. 1984), whereas Pintail diet in winter is composed mainly by seeds (Guillemain and Fritz 2002). Favouring seed bearing plant species and gastropods assemblages will benefit Shoveler and Pintail populations in Greek wetlands during winter, at least under their dietary needs' aspect. Coot is considered to be a herbivorous species consuming mainly stems and leaves from aquatic and terrestrial plants (Thomas 1982). However, Coot exhibits considerably foraging flexibility and it is also capable of consuming elevated amount of animals (Ponyi 1994, Perrow *et al*. 1997). In our study, Coot was based upon animal matter for food more than any of the studied *Anas* species did in the present study. However, the majority of the coot's gizzards were collected in the Messolonghi Lagoon, where all studied bird species consumed higher proportions of animal matter than in the other three areas. This means that in the other study areas there is a potential that animal matter is not as important for Coot as it is in Messolonghi Lagoon.

Seeds of the genus *Scirpus* are an important constituent in the diet composition of waterfowl (Green *et al*. 2002, Figuerola *et al*. 2003). *Ruppia maritima and R. cirrhosa* are widespread benthic angiosperms in Greek wetlands (Nicolaidou *et al*. 2005) and their biomass (seeds and green parts) constitutes a common food of various waterfowl species, including our studied species (Figuerola *et al*. 2002).

The use of invertebrates by waterfowl during the wintering season is usually low, in contrast to the pre-breeding and the nesting periods when consumption of animal matter by these birds is usually elevated due to their enhanced nutrient and energy requirements (Ankney and Afton 1988, Euliss *et al*. 1991, McKnight and Hepp 1998). Even though these were the general trends in the present study too, spatial variation in the consumption of the three major food categories by waterfowl was observed. Specifically, birds in Messolonghi Lagoon tend to feed upon different food resources (elevated *Ruppia* and animal consumption) compared to the other study areas, which is quite important in conservation efforts. It is well documented that for adaptable species, such as waterfowl, food availability is the principal factor influencing the use of potential foods (Euliss *et al*. 1991, Sanchez *et al*. 2000, Fritz *et al*. 2001) and the foraging strategy they follow in order to cope with regular or unexpected periods of food limitation (DuBowy 1997, Guillemain *et al*. 2000, Werner *et al*. 2005). *Ruppia* spp. are the dominant phytobenthic species in Messolonghi Lagoon (Wolff 1968) and this is probably the reason for their elevated consumption in this area.

Geographical variation in vegetation composition is a common phenomenon; thus, it is likely that intraspecific variation of food selection in herbivorous *Anatidae* between different wetlands also exists (Durant *et al*. 2006). The findings of the present study confirm this theoretical approach and give an incentive for future research in order to more deeply understand why birds behaved in such a way and especially to what extent these differences in diet composition within species among study areas are a consequence of variation of selectivity or of food availability. Of course, the selection of diets and wintering habitats by waterfowl is the ultimate outcome of the combined influence of several factors other than food availability, such as predation and hunting pressure, protection from adverse weather conditions, human disturbance, morphological and physiological intra - and inter - specific differences (Pöysä 1987, Guillemain *et al*. 2002a, 2002b, Paillisson *et al*. 2002, Durant *et al*. 2004), making relative model construction much more complex. Understanding the mechanisms dominating and defining the patterns of forage and habitat selection by waterfowl will make our predictions on the dynamics of plant-waterfowl communities more reliable and in consequence the holistic wetland conservation more realizable. At this stage however, providing increased habitat heterogeneity (a mosaic of grassy-weedy, halophytic, small-sized cropland sites, marshes and lakes with various water depths and salinity levels) will ensure high availability and diversity of both plants and invertebrate assemblages. This seems to be of the foremost importance for waterfowl species to meet their behavioural and nutritional requirements and subsequently for their effective conservation in Greek wetlands.

Acknowledgements – The Hellenic Ministry of Rural Development and Food is gratefully acknowledged for the financial support and especially Mr. Georgios Handrinos. The authors express gratitude to Tassos Anastassiadis, Eleni Makrigianni, Maria Noidou, Maria Panagiotopoulou, Fotis Pergantis, Vassilis Terzis and Yiannis Tsougrakis for their valuable help in the field and during the analysis. This study complies with the current Greek laws.

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