Diet and Feeding Habitats of Camargue Dabbling Ducks: What Has Changed Since the 1960s?

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Abstract.—In the Camargue (southern France), drastic changes in wetlands have occurred (notably extension of agriculture and salt extraction) since the 1960s, which affect the resources available to migratory waterbirds. Winter diets of Mallard (*Anas platyrhynchos*) and Teal (*A. crecca*) in 2006-2008 were assessed by analyses of gullet contents. Using PCA-based methods, duck diets were described and the main feeding habitats used by each duck species were then determined with a typology analysis. The same four food items were most important (in terms of occurrence and average dry weight) in the diet of Mallard and Teal: *Oryza sativa* (rice), *Echinochloa* sp., *Scirpus maritimus* and *Potamogeton pusillus* seeds. However, Teal diet was more diversified, with eleven feeding habitat types, compared to only five in Mallard. Both species were found to be dependent on ricefields and ricefield-like habitats. Compared to previous studies in the same area between 1964 and 1981, permanent freshwater habitats now appear to be used more intensively by Mallard and Teal, while temporary marshes are used to a lesser extent. Since the 1960s, temporary marshes have been partially replaced by permanent freshwater in order to attract more ducks, mostly for hunting. The flexibility of duck diet in response to changing food availability may explain why duck populations have not decreased in the Camargue or in Europe despite changes in land use. *Received 14 February*

Key words.—Diet comparison, feeding habitat, habitat use, land use, Mallard, Teal.

Habitat loss and land use change are important threats to wetlands. Wetland destruction and degradation are generally linked with human activities, especially through extension of agricultural, industrial and urban zones (Gibbs 2000; MWO 2012). At the same time, qualitative changes have occurred in wetlands, e.g. fish farming leading to eutrophication (Heathwaite 2010). In brackish waters, wetland management for hunting often involves inputs of freshwater, altering the natural water cycle (Tamisier and Grillas 1994) and potentially causing eutrophication and introduction of non-native species (MWO 2012).

Wetland loss or changes in land use have important consequences for waterbirds. Both processes alter distribution of food items and suitable habitat for ducks (Rendòn *et al.* 2008). For instance, agricultural practices can cause duck population declines at the local scale (e.g. Duncan *et al.* 1999). Wetland loss or land use changes may lead to a change in waterbird habitat selection and diet choice (Kloskowski *et al.* 2009).

The Camargue is a Mediterranean wetland in southern France of great importance to wintering waterbirds (Tamisier and Dehorter 1999). Since the 1950s, drastic habitat modifications have occurred owing to anthropogenic causes in the area. The loss of natural wetlands has been related to the extension of agriculture, salt extraction and industry (Tamisier and Dehorter 1999; MWO 2012). On most of the remaining wetlands (many being private hunting estates), management has involved dividing marshes into smaller units and inputs of freshwater, resulting in a decrease in water salinity and a lengthening of flooding duration (Tamisier and Grillas 1994). Increased area and permanence of marshes led to increases in biomass and changes in species composition of aquatic vegetation (Aznar *et al.* 2003), making the Camargue more attractive to waterbirds, despite changes in water management having a negative impact on the diversity of plants and invertebrates (Tamisier and Grillas 1994).

A better understanding of the relationship between ducks and their habitat will facilitate wetland management and allow prediction of the effects of future global change (Perry *et al.* 2007). In this study, we identified the current diet of the two most common wintering dabbling ducks in the Camargue, Mallard (*Anas platyrhynchos*) and Common Teal (*A. crecca*, hereafter Teal), by analyzing gullet contents. Owing to their nocturnal foraging, it was not practical to determine habitat use by direct monitoring of duck distribution over the Camargue. Therefore, we used the gullet contents to identify the feeding habitat types used by the ducks. Finally, we compared current diet descriptions with previous studies in 1979-81 (hereafter c.1980) for Mallard and in 1964-66 (hereafter c.1965) for Teal (Pirot 1981 and Tamisier 1971, respectively). The aim of this comparison was to assess how land use change in the Camargue has resulted in changes in the diet of these two species.

Methods

Study Area and Species

The Camargue encompasses approximately 145,000 ha, with 60,000 ha of natural wetlands and 85,000 ha of artificial habitats (Tamisier 1990). The surface area of the main types of habitats in the Camargue has changed since the 1940s, with expansion of salt pans, agricultural areas and industrial/urban areas at the expense of natural wetlands. Rice (*Oryza sativa*) is the primary crop of the Camargue. Protected areas represent 14% of the whole Camargue and 24% of the wetland area, salt pans included (Tamisier and Dehorter 1999). Hunting is permitted in all other wetland areas.

Tens of thousands of Mallard and Teal winter in the Camargue from August to March (annual peak counts ranging from 30,000 to 60,000 for each of the two species; Kayser *et al.* 2008). These species represent 20 to 30% of the total Camargue wintering duck population (Tamisier and Dehorter 1999). Because they are highly regarded as game, these ducks are among the principal drivers of wetland management for private hunting estates and nature reserves.

Sample Collection and Analysis

To avoid food items being subjected to physical breakdown in the gizzard, diet was inferred only from the contents of the esophagus and proventriculus (hereafter 'gullet'), as recommended by Swanson and Bartonek (1970).

Mallard and Teal gullets were collected from hunters at eight sites (Fig. 1) during the hunting seasons 2006-7 and 2007-8 (Table 1). Most ducks were shot in the early morning, when flying out of wetland feeding sites towards roosting sites, so that their gullet would likely contain food items consumed during the night (Tamisier and Dehorter 1999). In most cases (86%), the gullet was removed 1-7 h after the duck was shot (the remaining 13% were removed the day after, with the duck kept in the fridge meanwhile). Gullet samples were then frozen in a plastic bag until examination. After excluding those empty of food items (57 Mallard and 69 Teal gullets), a total of 119 Mallard and 302 Teal gullets were analysed in the laboratory, where samples were washed through a 63-µm sieve. The retained material was sorted under a binocular microscope. The content of each gullet was separated into invertebrates, 'seeds' (i.e. achenes, oogonia and proper seeds) and plant vegetative parts. As the latter represented less than 0.2% of the average relative dry weight of the gullet contents in both duck species (Table 2), they were discarded from the statistical analyses. Invertebrates were identified using Tachet *et al.* (2000) or local specialists, to the family level in most cases. Seeds were mostly identified to genus or species using Campredon *et al.* (1982), Cappers *et al.* (2006), and a local reference collection. Invertebrates and seeds (hereafter "food items") in small numbers were counted individually, whereas the number of abundant food items was esti-

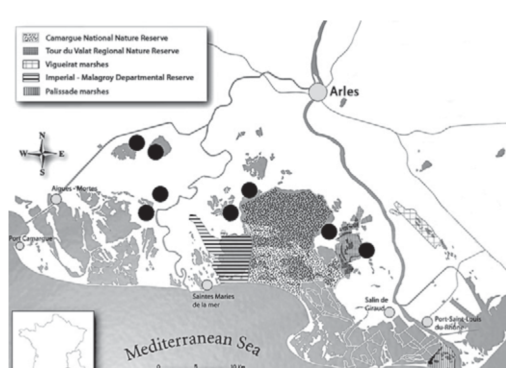


Figure 1. The Camargue showing the eight collection sites for gullet samples (black symbols) and the five main protected areas.

Table 1. Number of gullet samples collected each month during the winters 2006-07 and 2007-08 for Mallard and Teal. Empty gullets are excluded.

	Mallard		Teal	
	2006-07	2007-08	2006-07	2007-08
September	6	35	17	41
October	12	16	32	30
November	8	8	34	13
December	10	11	24	41
January	7	6	34	36
TOTAL	43	76	141	161
	119		302	

mated by subsampling. Seed specific dry weights were taken from Arzel *et al.* (2007), complemented by our own measurements for those species not given by these authors, following the same method they used. We also used the protocol of Arzel *et al.* (2007) to measure the dry weight of invertebrates.

Statistical Analyses

We assumed that the hunting of ducks in Camargue is equivalent to random sampling in a large population. Data were presented as two distinct matrices in each species for the number and the dry weight of each food item type, respectively. Let $\mathbf{O} = [o_{ij}]$ be the $n \times m$ matrix for one duck species with o_{ij} the number of occurrences of the jth food item (columns, $1 \leq j \leq m$, with m the total number of food items) in the ith gullet (rows, $1 \leq i \leq n$) and $\mathbf{W} = [w_{ij}]$ the $n \times m$ matrix for one duck species with w_{ij} the dry weight of the jth food item (columns, $1 \leq j \leq m$) in the ith gullet (rows, $1 \leq i \leq n$). Two statistics were used to summarize the contribution of food items to the diet of each duck species: (i) Ro_j the relative frequency of occurrence of the jth food item ($1 \leq j \leq m$,) in gullets, ($Ro_j = n^{-1}\sum_{i=1}^{n} o_{ij}$) i.e. the mean number of occurrences of the jth food item among gullets, expressed as percentage (see Table S1); (ii) Rw_j the average relative dry weight of the jth food item ($1 \leq j \leq m$) among gullets ($Rw_j = n^{-1}\sum_{i=1}^{n} p_{ij}$ with $p_{ij} = w_{ij} / \sum_{j=1}^{m} w_{ij}$), i.e. calculated by dividing the dry weight of each food item in each gullet by the total dry weight of all food items in the same gullet, then taking the average over all individuals, expressed as percentage (see Table S1 and S2).

PCA-based analyses

Let $\mathbf{P} = [p_{ij}]$ be the $n \times m$ matrix of row profiles for one duck species with $p_{ij} = w_{ij} / \sum_{j=1}^{m} w_{ij}$ the proportion ($0 \leq p_{ij} \leq 1$) of the jth food item (columns, $1 \leq j \leq m$) in the ith gullet (rows, $1 \leq i \leq n$). For both duck species, the matrices **P** were analyzed by performing a column-centered principal component analysis (%PCA, sensu de Crespin de Billy *et al.* 2000). We analyzed diet composition by examining the first two principal components of the column-centered PCA on distance biplots (see Storms *et al.* 2008 for details). Specific interpretation rules arise from the compositional nature of the **P** matrix (see de Crespin de Billy *et al.* 2000; Storms *et al.* 2008).

We performed separate %PCAs for Mallard and Teal. We tested for a winter (i.e. year) effect on diet composition using a between-class %PCA and its associated randomization test (see Storms *et al.* 2008 for details), and found no biologically relevant effect for Mallard (between-class inertia to total inertia ratio R = 0.0073, $P = 0.5$) nor for Teal (R = 0.0068, $P = 0.022$). We therefore decided to pool data from both winters for each duck species for subsequent analyses.

We tested for a seasonal effect (early winter: September and October; late winter: November to January) on diet composition. These two periods correspond to the first two periods (out of three) of the duck "wintering strategy" in the Camargue (restoring, pairing and fattening periods) during which feeding time budgets differ (Tamisier *et al.* 1995). We found some statistical evidence for a seasonal effect in both species, with comparable effect sizes ($P = 0.033$ and 0.000001, R = 0.020 and 0.025 for Mallard and Teal, respectively). Although the size of the effect was small, we decided to perform separate %PCAs for early and late winter for both species, as feeding times and habitat selection may change between these two periods of the winter (Tamisier *et al.* 1995), hence potentially influencing duck diet and feeding habitats. Computations and graphical displays were performed using the 'ade4' package for R (Chessel *et al.* 2004).

Food item typology analysis

For establishing stable typologies, we had to make the matrices **W** less sparse (a sparse matrix contains a high proportion of zeros) than they were initially. Hence, in a first step, for each species we derived a $n \times m$ matrix $\mathbf{Z} = [z_{ij}]$ from $\mathbf{W} = [w_{ij}]$, where $z_{ij}=1$ if $w_{ij} > 0$, and $z_{ij}=0$ otherwise. We sorted the columns (food items) by decreasing order of proportion of 1s (by referring to the total number of 1s in the matrix), and we kept the columns until we reached a cumulative sum of 85%. We thus obtained a $n \times m'$ matrix **Z'** ($m' < m$). We followed the same procedure for the rows (gullets) of **Z'**,

Table 2. Average relative dry weight (*Rw* expressed in percentage) of the main food types (invertebrates, seeds and vegetative parts of plants) and main food items according to %PCA diet analysis (see Methods: '*PCA-based analyses*' section and Results), for both Mallard (*n* = 119) and Teal (*n* = 302).

Food item	Mallard	Teal
Invertebrates	6.2	15.6
Seeds	93.7	84.3
- *Oryza sativa*	35.1	8.5
- *Echinochloa* sp.	22.2	14.0
- *Scirpus maritimus*	5.8	17.3
- *Potamogeton pusillus*	7.2	7.9
- *Potamogeton nodosus*	4.1	—
- *Triticum aestivum*	5.4	—
- *Chara* spp.	—	6.0
- *Suaeda* sp.	—	3.6
Vegetative parts	<0.1	0.2

for a cumulative sum up to 95%, removing gullets that contained ≤ 1 food item, i.e. 12% and 15% of Mallard and Teal gullets, respectively. Except for four Mallards and two Teal that specialised on one food item (mean seed number per gullets: 142 and 123 for Mallard and Teal respectively), all other gullets contained less than 18 seeds. We obtained an $n' \times m'$ matrix **W'** ($n' < n$, $m' < m$), maintaining about 80% of the values $w_{ij} > 0$ (81% for Mallard and 82% for Teal) and increasing considerably the filling rate of the matrices (from 2% to 16% for Mallard, and from 5% to 19% for Teal). In a second step, we used hierarchical agglomerative clustering, with chi-squared distance between the column profiles (e.g. Lebart *et al.* 2000) as the underlying distance function, and the Ward method (e.g. Legendre and Legendre 1998) to determine distances between clusters. In calculating the Ward criterion, we employed its generalized formula (e.g. Lebart *et al.* 2000), using the weights of the column profiles (i.e. the $Rw'_j / \sum_{j=1}^{m} Rw'_j$, $1 \le j \le m'$). We obtained a dendrogram for each species, which was truncated (the level of truncation was chosen visually), leading to a partition of the food items into *k* clusters (or classes). In a third step, we computed (i) the centroids of the classes (the food items were weighted as previously), (ii) the chi-square distances between the centroids of the classes, and (iii) the chi-square distance between each food item and the centroid of its class (which allows identification of the food items most characteristic of each class). To improve visibility, all the chi-square distances hereafter mentioned were multiplied by 10,000.

Relative importance of the food item classes

After the typology was built and characterized, we were interested in identifying the classes involving the most individuals (i.e. most gullets). For the *i*th individual ($1 \le i \le n'$), we calculated the total dry weight for the *j*th class of food items, which was then divided by the total dry weight of the *k* classes, leading to the proportion p'_{ij} ($0 \le p'_{ij} \le 1$). By repeating for $1 \le j \le k$ we obtained the row profile $s_i = \underbrace{[p'_{i1}, p'_{i2}, \ldots, p'_{ik}]}_{k\ columns}$. In the hypothetical case where a gullet *i* was full of the food items of one unique class *j* ($j = 1,2, \ldots, k$), then the corresponding row profile would be, respectively:

$$t_1 = \underbrace{[1,0,\ldots0]}_{k\ columns},\ t_2 = \underbrace{[1,0,\ldots0]}_{k\ columns},\ t_k = \underbrace{[0,0,\ldots0]}_{k\ columns}.$$

Hence, we computed the chi-square distances between the *i*th row profile s_i ($1 \le i \le n'$) and the hypothetical row profiles t_1, t_2, …, t_k, and the *i*th individual was assigned to the closest class *j*. Finally, we calculated the percentages of individuals assigned to each of the *k* classes.

Diet diversity

Diet diversity was measured by calculating Simpson's index of diversity for each gullet as, $S'_i = 1 - S_i$, with Simpson's index $S_i = \sum_{j=1}^{m} p^2_{ij}$ (see Storms *et al.* 2008 for interpretation). For each species (Mallard / Teal) and each period (early winter / late winter), we estimated the sampling distribution of the mean diet diversity by *bootstrapping* (e.g. Efron and Tibshirani 1993). We used 10^6 bootstrap samples to accurately estimate the sampling distributions in each of the four groups (Mallard / early winter, Mallard / late winter, Teal / early winter, Teal / late winter). The four sampling distributions were plotted together (Fig. 2).

Results

Mallard Diet

A total of 69 food item types were recorded in Mallard diet (see Table S1). %PCA diet analysis (based on *Rw*) was based on the examination of the first two axes, accumulating 51% and 59% of total inertia in early and late winter, respectively, and showed food items and gullets simultaneously (distance biplot on Fig. 3). According to Fig. 3, Mallard diet was mainly composed, in decreasing order of importance, of *O. sativa*, *Echinochloa* sp., *Potamogeton pusillus*, *Scirpus maritimus* and *Potamogeton nodosus* in early winter (Fig. 3a), and by *O. sativa*, *Echinochloa* sp., *Triticum aestivum* (wheat) and *S. maritimus* in late winter (Fig. 3b). For clarity, only the most important food items were labelled on the distance biplots. The six most consumed items represented almost 80% of diet by *Rw* over the whole winter period (Table 2). The sum of

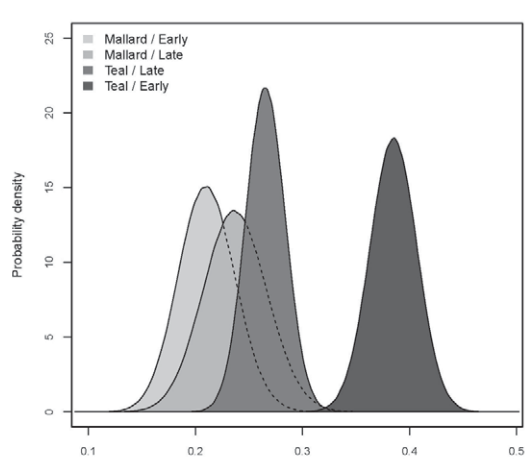


Figure 2. Sampling distributions of the mean diet diversity (Simpson's index of diversity) estimated by bootstrapping for the four groups: Mallard / early winter, Mallard / late winter, Teal / early winter, Teal / late winter (see Methods: 'Diet diversity' section and Results).

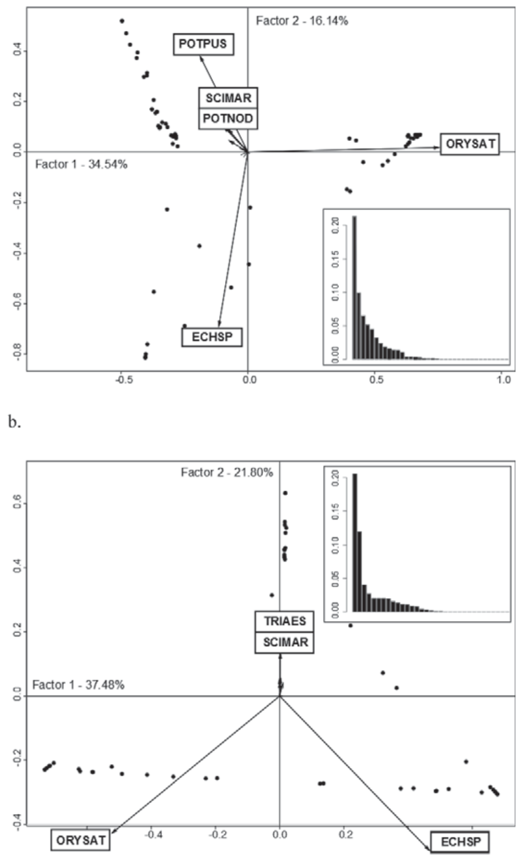


Figure 3. Column-centered PCA screeplot (histogram) and distance biplot (graph) of gullet contents of Mallards (points show different individuals), for (a) early and (b) late winter, according to food items (arrows), on the first factorial plane (ECHSP: *Echnichloa* sp., ORYSAT: *Oryza sativa*, POTNOD: *Potamogeton nodosus*, POTPUS: *Potamogeton pusillus*, SCIMAR: *Scirpus maritimus*, TRIAES: *Triticum aestivum*).

O. sativa and *Echinochloa* sp. accounted for more than 57% of *Rw*, with these seeds being found in 69% of gullets (*Ro*). Seeds of *T. aestivum* and *P. nodosus* were consumed in large quantities, but by a relatively small proportion of Mallards (*Ro* 8 and 10% respectively). Other cultivated species were also found in Mallard gullets, but at lower abundance and occurrence: Sunflower *Helianthus annuus* (*Ro* 0.8%, *Rw* < 0.1%), Millet *Milium* sp. (*Ro* 3%, *Rw* 0.4%), Sorghum *Sorghum* sp. (*Ro* 3%, *Rw* 0.7%), Maize *Zea mays* (*Ro* 2%, *Rw* 0.9%) and Grape *Vitis vinifera* (*Ro* 0.8%, *Rw* <0.1%). Plant seeds from brackish habitats, such as *Salicornia* sp. (*Ro* 0.8%, *Rw* 0.8%) and *Suaeda* sp. (*Ro* 3%, *Rw* 0.2%), had low frequencies and abundance in Mallard gullets. We also observed exotic seed species, such as *Ludwigia peploides* (*Rw* 0.7%), *Eleusine indica* (*Rw* < 0.1%), *Paspalum distichum* (*Rw* < 0.1%) and *Heteranthera reniformis* (*Rw* < 0.1%). Although Mallard diet was dominated by seeds, in terms of *Ro*, gastropods were found globally in 45% (N = 54) of gullets (*Ro* 25%, 31% and 8% for Physidae, Planorbidae and other unidentified gastropods, respectively).

In the food item typology analysis, five classes were obtained (Table 3). *O. sativa*, *P. nodosus*, *Echinochloa* sp., *Polygonum* sp. and *T. cestivum* were the most characteristic food items of these classes (for class 1 to 5, respectively). The Chi-square distance matrix between barycentres of each class showed that classes characterised by *O. sativa*, *Echinochloa* sp. and *T. aestivum* were very close to each other (Chi-square distance: 25.86 between *O. sativa* and *Echinochloa* sp. classes, 38.09 between *O. sativa* and *T. aestivum* classes, and 39.37 between *Echinochloa* sp. and *T. aestivum* classes; all other Chi-square distances > 103.67). Fifty six percent of sampled Mallard were assigned to the *O. sativa* class, 27% to the *Echinochloa* sp. class and 10% to the *P. nodosus* class. Class 4 represented 1% of ducks and corresponded to a few Mallards having consumed one main food item (*Polygonum* sp.) in large quantities, plus some other less numerous food items. Class 5 represented 6% of ducks and corresponded to a few Mallards having consumed one main food item (*T. aestivum*) in large quantities, plus some other less numerous food items.

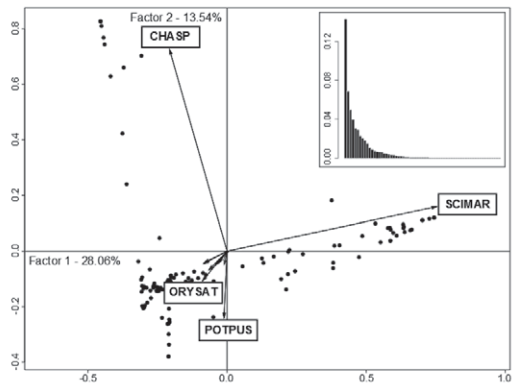
Teal Diet

A total of 103 food item types were recorded in Teal diet (see Table S1). %PCA diet analysis (based on average relative dry weight) was based on the examination of the first two axes, accumulating 42 and 32% of total inertia in early and late winter, respectively, and showed food items and gullets simultaneously (distance biplot on Fig. 4). According to Fig. 4, Teal diet was principally composed, in decreasing order, of *S. maritimus*, *Chara* spp., *P. pusillus* and *O.sativa* in early winter (Fig. 4a), and by *Echinochloa*

Table 3. Results of food item typology analysis for Mallard (the row in the Table S1, preceded by "r", is given in brackets). Chi-square distance (× 10 000) of each food item from the centroid of that class is given (see Methods: 'Food item typology analysis' section). The food item in bold is the closest to the centroid.

Class	Food item	Distance between a food item and centroid of its class 1	2	3	4	5	% individuals per class
1	Oryza sativa (r86)	**0.5**					55.7
	Chara sp. (r46)	54.4					
	Physidae (r35)	57.8					
	Coleoptera (adult and larvae) (r14)	73.9					
	Schoenoplectus mucronatus (r61)	82.7					
	Odonata (larvae) (r33)	90.6					
	Scirpus maritimus (r62)	90.8					
	Planorbidae (r36)	108.1					
	Gasteropoda (r37)	153.1					
	Najas indica (r73)	155.9					
	Najas minor (r75)	158.7					
	Cyathura carinata (r6)	275.34					
	Potamogeton pectinatus (r107)	451.9					
	Myriophyllum spicatum (r66)	967.2					
2	**Potamogeton nodosus** (r106)		**477.7**				10.3
	Potamogeton pusillus (r108)		517.8				
	Ludwigia peploides (r77)		567.8				
	Oryza sativa (receptacles) (r86)		1228.8				
3	**Echinochloa sp.** (r80)			**0.5**			26.8
	Polygonum lapathifolium (r100)			59.4			
	Setaria verticillata (r92)			76.1			
	Rumex sp. (r103)			163.5			
	Eleocharis palustris (r59)			311.8			
4	**Polygonum sp.** (r102)				**1.6**		1.0
5	**Triticum aestivum** (r95)					**0.4**	6.2
	Polygonum persicaria (r101)					128.3	

sp., *S. maritimus*, *O. sativa*, *Suaeda* sp. and *P. pusillus* in late winter (Fig. 4b). For clarity, only the most important food items were labelled on the distance biplots. The six most consumed items represented almost 60% of diet by *Rw* over the whole winter period (compared to 80% in Mallard; Table 2). With the exception of *Suaeda* sp., each of these food items contributed more than 5% to *Rw* over the whole wintering period. *S. maritimus*, *Echinochloa* sp., and *O. sativa* seeds alone accounted for about 40% of *Rw*. *Chara* spp. were very frequent in Teal diet with a *Ro* of 36%. However, only 4% of Teal consumed this food item in large quantities, i.e. with more than 16,000 *Chara* oogonia in the gullet. In 56% of cases, *Chara* spp. were associated with a large number of *Echinochloa* sp. seeds in the gullets. *Suaeda* sp. was among the main food items, although *Ro* of this taxon was only 13%. However, this taxon was consumed in large quantities (with more than 2,000 seeds in the gullets) by a few Teal (2% of gullets). *Suaeda* sp. was more frequently present in smaller numbers and in association with seeds of *Chara* spp., *Zannichellia* sp. (*Rw* 0.5%) and *Phragmites australis* (*Rw* 0.8%). *E. palustris* was not a major food item for Teal, but represented 20% of *Ro* and 3% of *Rw*. Other seed species, such as *H. reniformis* (*Ro* 12%, *Rw* 0.4%), *L. peploides* (*Ro* 13%, *Rw* 2%), *Zannichellia* sp. (*Ro* 14%, *Rw* 0.5%), *Schoenoplectus mucronatus* (*Ro* 14%, *Rw* 1%) and *Najas* spp. (*Ro 28%*, *Rw* 2%), did not contribute much to the average diet in terms of dry weight, but occurred relatively frequently. As for Mallards, cultivated species other than *O. sativa* and



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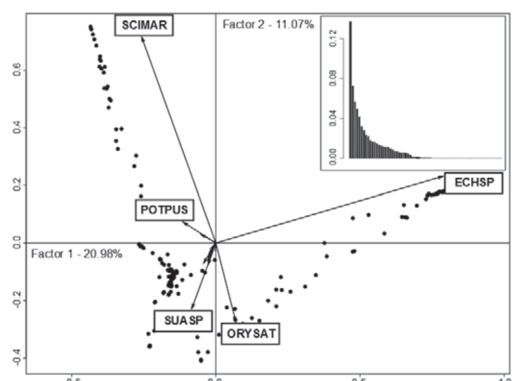

Figure 4. Column-centered PCA screeplot (histogram) and distance biplot (graph) of gullet contents of Teal (points show different individuals), for (a) early and (b) late winter, according to food items (arrows), on the first factorial plane (CHAPSP: *Chara* spp., ECHSP: *Echnichloa* sp., ORYSAT: *Oryza sativa*, POTPUS: *Potamogeton pusillus*, SCIMAR: *Scirpus maritimus*, and SUASP: *Suaeda* sp.).

T. aestivum were found in Teal diet: *Milium* sp. (*Rw* 2%) and *Sorghum* sp. (*Rw* 1%). Finally, Teal were less granivorous and more dependent on invertebrates than Mallards. Gastropods represented 9% of *Rw*. Diptera, while contributing only 4% of *Rw*, contributed 34 % of *Ro* (see Table S1 for details).

Based on food item typology analysis, eleven classes were obtained (Table 4). The most characteristic food items of these classes (for class 1 to 11, respectively) were *Suaeda* sp., Ceratopogonidae, *H. reniformis*, *P. distichum*, *Chara* spp., *Najas minor*, Physidae, *Echinochloa* sp., *O. sativa*, *Salicornia* sp., and *T. aestivum*. The Chi-square distance matrix between barycentres of each class showed that *Suaeda* sp, *Echinochloa* sp., and *O. sativa* classes were the closest, compared to the others (Chi-square distance: 36.89 between *Suaeda* sp.and *Echinochloa* sp. classes, 39.45 between *Echinochloa* sp. and *O. sativa* classes, and 45.83 between *Suaeda* sp. and *O. sativa* classes; all others Chi-squares > 54.21). 55% of sampled Teal were assigned to the *O. sativa* class, 18% to the *Echinochloa* sp. class and 8% to the Physidae class. Classes gathering less than 5% of ducks corresponded to few Teal having consumed only one main food item, but in very large quantities, plus some other less numerous food items.

Diet Diversity

Diet diversity analyses (Fig. 2) showed that mean diet diversity differed between seasons for Teal, but not for Mallard (peaks in mean diversity overlapping with each other). The mean diet diversity differed significantly between species but diversity was significantly greater for Teal in early winter, while there was no significant difference in late winter.

Discussion

The same four food items were most important (in terms of frequency of occurrence *Ro* and average dry weight *Rw*) in the current diet of Mallard and Teal, though in a different order of importance: *O. sativa*, *Echinochloa* sp., *S. maritimus* and *P. pusillus* seeds. Combined, they represented 70% of Mallard average diet by *Rw* but only 48% for Teal. The two former items dominate the diet of Mallard, and the two latter the diet of Teal. Among these principal items, *O. sativa* is a cultivated species and *Echinochloa* sp. and *S. maritimus* are the two most common rice weeds in the Camargue (Marnotte *et al.* 2006). The importance of these four food items in both duck diet reflects the extreme dependence of both species on cultivated habitats in the Camargue, although *S. maritimus* is also common in brackish marshes (Molinier and Tallon 1974).

Here, we focus on our results for seeds, since these food items were usually identi-

Table 4. Results of food item typology analysis for Teal (the row in the Table S1, preceded by "r", is given in brackets). Chi-square distance (× 10 000) of each food item from the centroid of that class is given (see Methods: 'Food item typology analysis' section). The food item in bold is the closest to the centroid.

Class	Food items	Distance between a food item and centroid of its class											% individuals per class
		1	2	3	4	5	6	7	8	9	10	11	
1	***Suaeda* sp.** (r53)	**0.1**											3.7
	Psychodidae (larvae) (r18)	45.4											
	Phragmites australis (r89)	48.4											
2	**Ceratopogonidae (larvae)** (r15)		**13.9**										2.9
	Ostracoda (r9)		104.2										
3	***Heteranthera reniformis*** (r105)			**5.4**									0.4
4	***Paspalum distichum*** (r88)				**19.7**								2.0
5	***Chara* sp.** (r46)					**4.3**							2.9
	Cladocera (ephippia) (r5)					121.6							
	Juncus sp. (r67)					194.9							
6	***Najas minor*** (r75)						**21.1**						0.4
7	**Physidae** (r35)							**16.0**					8.0
	Polygonum lapathifolium (r100)							184.6					
	Ludwigia peploides (r77)							229.3					
	Inula sp. (r55)							266.0					
8	***Echinochloa* sp.** (r80)								**1.00**				18.3
	Hydrachnellae (r1)								57.1				
	Schoenoplectus mucronatus (r61)								63.7				
	Polygonum persicaria (r101)								68.7				
	Diptera (adult, nymph and larvae) (r24)								94.7				
	Gasteropoda (r37)								100.0				
	Anisoptera (larvae) (r31)								199.9				
	Oryza sativa (embases) (r86)								216.8				
	Coleoptera (adult and larvae) (r14)								226.4				
9	***Oryza sativa*** (r86)									**6.6**			54.5
	Planorbidae (r36)									58.2			
	Najas indica (r73)									77.1			
	Odonata (larvae) (r33)									86.3			

Table 4. (Continued) Results of food item typology analysis for Teal (the row in the Table S1, preceded by "r", is given in brackets). Chi-square distance (×10 000) of each food item from the centroid of that class is given (see Methods: 'Food item typology analysis' section). The food item in bold is the closest to the centroid.

Class	Food items	Distance between a food item and centroid of its class											% individuals per class
		1	2	3	4	5	6	7	8	9	10	11	
	Scirpus maritimus (r62)									95.5			
	Chironomidae (larvae) (r16)									144.7			
	Potamogeton pusillus (r108)									211.8			
	Eleocharis palustris (r59)									223.89			
	Hydrophilidae (larvae) (r12)									224.1			
	Cyperus difformis (r58)									418.7			
	Myriophyllum spicatum (r66)									699.9			
	Ranunculus sp. (r109									765.1			
10	***Salicornia* sp.** (r51)										**8.7**		1.2
11	***Triticum aestivum*** (r95)											**2.8**	5.7
	Zannichellia sp. (r116)											139.3	

fied to the species level, permitting identification of more precise feeding habitat, contrary to invertebrate taxa which could mostly be identified at the family level. The presence in duck diets of rice and typical rice weeds (e.g. *E. palustris*, *Polygonum lapathifolium*, *Polygonum persicaria*, *Cyperus difformis*, and *S. mucronatus*; Marnotte *et al.* 2006) either in isolation, mixed together, or sometimes also mixed with hydrophyte seeds, which are typical of permanent (*Potamogeton pectinatus*, *Myriophyllum spicatum*) and semi-permanent (*P. nodosus*, *P. pusillus*) freshwater marshes, may also result from different hunting management strategies. Baiting is a common strategy used by hunters in the Camargue. Bait can be composed of rice, rice weeds or both, depending on whether bait comes from unsorted or sorted harvest or from harvest waste. The presence of *P. pectinatus* in Mallard diet and *P. pusillus* in Teal diet, mixed with other species characteristic of ricefield habitat, may result from rice bait being spread in pondweed marshes (authors' personal observation). Alternatively, the presence of rice in duck diet could also reflect the exploitation of post-harvest ricefields by ducks during winter, either when these are naturally flooded by rain or specifically managed as freshwater habitat in order to attract waterfowl (Elphick and Oring 1998; Tourenq *et al.* 2001). These two management strategies (i.e. bait or ricefield management) are both practiced in the Camargue and represent part of the habitat change there, but they could not be differentiated by duck diet analysis alone. Wheat in duck diet was also likely to be from hunting bait, since this species is not cultivated during winter in the Camargue, and wheat seeds rot rapidly when moist (authors' personal observation). The association of wheat with other plant species from a different habitat (*P. persicaria* and *Zanichellia* sp. for Mallard and Teal, respectively) in the same typology class may result from the use of wheat bait in freshwater marshes.

Besides the four common most numerous food items, important differences were observed between the current diets of the two duck species, such as the heavy consumption of *Chara* oogonia by Teal and of *P. nodosus* seeds by Mallard. Overall, a greater diversity of food items was observed in Teal. Mallard are known to select larger food items on average than Teal, although both use a broad range of seed sizes (Guillemain *et al.* 2002; Brochet *et al.* 2012). Pöysä (1987) suggested the diverse use made by Teal of habitats in the horizontal dimension was associated with a varied diet. Conversely, the restricted use of shorelines by Mallards was associated with a less variable diet (see also Nummi 1993). Furthermore, in our study Teal also seemed to be less dependent on ricefields than Mallard, but more dependent on semi-permanent freshwater marshes. Mallard appeared to largely specialize on rice and associated plant species (57% of the average Mallard diet by *Rw* is composed by *O. sativa* and *Echinochloa* sp.). In the Ebro delta, northern Spain, rice was also found to be more frequent in the diet of Mallard than of Teal (Mateo *et al.* 2000).

Brackish habitats were represented in Teal diet by only one class characterized by *Suaeda* sp., a typical species of shallow, brackish habitats. Characteristic seed species of temporary freshwater or brackish habitats (e.g. *Ruppia* sp., *Chara* sp. or *Zannichellia* sp.), or coastal lagoon habitat (e.g. *Zostera noltii*) may have been slightly underestimated in our duck diet study. These habitats in the Camargue correspond mainly to protected areas where management is less intensive, and marshes are more salty due to natural marine influence (most protected areas are in the South of Camargue, near the Mediterranean Sea) and some brackish and/or annual plants are more abundant there than in permanent freshwater habitats (Tamisier and Dehorter 1999). Ducks using protected areas for both feeding and resting were not represented in our analysis, as they escape hunting pressure. These individuals however likely represent a minor part of the duck population, since Camargue wintering ducks generally commute twice daily between a day-roost and a distinct nocturnal foraging area (Tamisier and Dehorter 1999).

Mallard and Teal diets were previously studied in c.1980 by Pirot (1981) and in c.1965 by Tamisier (1971), respectively. The methods used were similar to ours (diet from hunted ducks; relative dry weight of food items), except that Tamisier (1971) also used a combination of gullet and gizzard contents.

In c.1980, Pirot (1981) found that Mallard diet in the Camargue was made up by *Rw* of 46% Poaceae (*O. sativa* and *Echninochloa* sp.), 17% Cyperaceae, 17% Chenopodiaceae, 14% Characeae, and 6% Potamogetonaceae (see also Green *et al.* 2002 for a detailed summary in English of this French reference). The equivalent proportions of these food items in our results were *Rw* 57%, 7%, 1%, <0.1% and 13% respectively. According to Pirot (1981), in c. 1980, Characeae were principally consumed at the beginning of winter and Cyperaceae at the end. *O. sativa*, *Echinochloa* sp., *S. maritimus* and *P. pectinatus* made up the main diet of Mallard throughout the period, the latter two being less abundant than the former two species. In c. 1980, the animal part was less than 1% of the average Mallard diet by *Rw*, whereas this part represented 6% in our results. Therefore, compared to c.1980, Mallard diet has not changed a great deal, rice and rice weeds still being the main food items. However we did notice a shift from *P. pectinatus* to *P. nodosus*, the former changing from a *Ro* of 33% in c. 1980 to 7% currently, and the latter from 0% to 10%. We also observed a lower consumption of *Chara* spp. in our study, *Rw* <1%, compared to 14% in Pirot (1981). In both studies, Mallard was dependent on ricefield habitats. *O. sativa* and *Echninochloa* sp. represented 46% by *Rw* in Pirot (1981) and 57% in our study, but ricefield surface area has increased over time (from c. 6,000 ha in 1980 to c. 20,000 ha from 2000-2010; Marnotte *et al.* 2006).

In c.1965, Tamisier (1971) found that Teal diet in the Camargue was made up, by *Rw*, of 25% Characeae, 25% Cyperaceae seeds and 25% seeds of *O. sativa* and *Echinochloa* sp. The last 25% consisted of Chenopodiaceae, Potamogetonacae, Ruppiacae and *Myriophyllum* sp. seeds. The equivalent proportions of these food items in our results were *Rw* 6%, 23%, 23%, and 17% respectively. Hence, Teal diet has not changed a great deal either since c.1965. However, the proportions of *Echinochloa* sp. and *S. maritimus* have increased over time (from 7% to 14% and from 4% to 17% respectively by *Rw*), whereas the proportions of Characeae and Ruppiaceae have decreased (from 23% to 6% and from 4% to 0.4%, respectively, by *Rw*). Teal now seem to exploit brackish and temporary freshwater habitats to a lesser extent than they did in the 1960s: *Suaeda* sp., *Chara* spp. and *Ruppia* sp. represented 27% of Teal diet by *Rw* in Tamisier (1971), and 10% in this study. The surface area of temporary brackish marshes has greatly decreased, most being replaced by permanent and semi-permanent freshwater marshes artificially flooded (Tamisier and Grillas 1994). Conversely Teal now seem to rely more on freshwater habitats (natural or cultivated): Poaceae, Potamogetonaceae and Haloragaceae represented 29% of Teal diet by *Rw* in Tamisier (1971) and 41% in this study. Ricefield surface area reached a peak of 32,500 ha in 1962 (29,500 ha in 1965, Marnotte *et al.* 2006), but there were also more temporary freshwater habitats then than nowadays. The surface area of temporary freshwater marshes declined by 60% from 1942 to 1984, and this trend continues (Tamisier and Dehorter 1999).

We also observed new food items that appeared in the diet of both ducks since c. 1965. First, we observed seeds of the exotic plants *H. reniformis* and *L. peploides*, native to the Americas, which colonized the Camargue 15 and 30 years ago, respectively (Marnotte *et al.* 2006). *H. reniformis* had a particularly high abundance in some Teal in this study, with up to 148,000 seeds in one gullet. Ducks are likely to play a role in the spread and colonization of new habitats by these plant species (Brochet *et al.* 2009, 2010). Secondly, we observed the appearance of indigenous plants such as *P. nodosus*, which was absent from previous diet studies, whereas this species was abundant and frequent in ours. *P. nodosus* was rare in the Camargue in the 1960s and known only from canals and ditches (Molinier and Tallon 1974). In the 1980s *P. nodosus* was not found in freshwater marshes (Britton and Podlejski 1981; Grillas 1990), but was still frequent in canals. *P. nodosus* was eventually found in year 2000 in freshwater Camargue marshes (Aznar *et al.* 2003), where this species is now widespread. There may be a parallel between the decline of *P. pectinatus* and the increase in both *P. nodosus* and *P. pusillus*. This switch may be due to a change in frequency of drought or drawdown (short and regular nowadays, long and irregular in the 1960s). More intensive water management developed for hunting activity (Tamisier and Dehorter 1999) may have favoured the latter two *Potamogeton* species. Conversely, we observed the disappearance of *Scirpus littoralis*, which was no longer recorded in the current Teal diet. *S. littoralis* was widespread at the beginning of the 1960s (Molinier and Tallon 1974; Britton and Podlejski 1981). Today the species is declining, with few known localities in the Camargue, likely due to intensification of marsh management, leading to eutrophication and frequent mechanical destruction of helophytes (P. Grillas, pers.comm.).

Our results indicate that the current diet of both Mallard and Teal rely essentially on cultivated species and associated plants. Most marshes of the Camargue are managed in order to attract the maximum number of waterbirds, mostly for hunting, but also partly for conservation and tourism purposes. Our results suggest that this intensive marsh management does not reach its goal, since ducks still principally exploit cultivated habitat. However, the switch from temporary to more permanent marshes has resulted in profound changes in plant species composition over the last decades, with an overall loss in plant biodiversity across the Camargue (Tamisier and Grillas 1994). This loss of natural wetland habitat does not seem to have affected Mallard and Teal abundance, since the size of their populations did not undergo a significant reduction since the 1970s, neither in the Camargue (Kayser *et al.* 2008) nor at wider scales across Europe (Delany and Scott 2006).

Acknowledgments

We are grateful to hunting managers who authorised us to take samples from ducks. We thank J. Fuster for help collecting gullet samples and L. Cosneau, M. Droulin and V. Pavési for help analysing gullet contents.

E. Coulet and A. Waterkeyn identified invertebrates. P. Grillas commented on the manuscript. A.-L. Brochet was funded by a Doctoral grant from Office National de la Chasse et de la Faune Sauvage, with further funding from a research agreement between ONCFS, the Tour du Valat, Laboratoire de Biométrie et de Biologie Evolutive (UMR 5558 CNRS Université Lyon 1) and the Doñana Biological Station (EBD-CSIC). Additional funding was received from Agence Interorganismes pour la Recherche et le Développement (AIRD) and MAVA Foundation.

Literature Cited

Arzel, C., J. Elmberg, M. Guillemain, P. Legagneux, F. Bosca, M. Chambouleyron, M. Lepley, C. Pin, A. Arnaud and V. Schricke. 2007. Average mass of seeds encountered by foraging dabbling ducks in Western Europe. Wildlife Biology 13: 328-336.

Aznar, J. C., A. Dervieux and P. Grillas. 2003. Association between aquatic vegetation and landscape indicators of human pressure. Wetlands 23: 149-160.

Britton, R. H. and V. D. Podlejski. 1981. Inventory and classification of the wetlands of the Camargue (France). Aquatic Botany 10: 195-228.

Brochet, A. L., L. Dessborn, P. Legagneux, J. Elmberg, M. Gauthier-Clerc, H. Fritz and M. Guillemain. 2012. Is diet segregation between dabbling ducks due to food partitioning? A review of seasonal patterns in the Western Palearctic. Journal of Zoology 286: 171–178.

Brochet, A. L., M. Guillemain, H. Fritz, M. Gauthier-Clerc and A. J. Green. 2009. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. Ecography 32: 919-928.

Brochet, A. L., M. Guillemain, H. Fritz M. Gauthier-Clerc and A. J. Green. 2010. Plant dispersal by teal (*Anas crecca*) in the Camargue: Duck guts are more important than their feet. Freshwater Biology 55: 1262–1273.

Campredon, S., P. Campredon, J. Y. Pirot and A. Tamisier. 1982. Manuel d'Analyse des Contenus Stomacaux de Canards et de Foulques. ONC, Paris, France.

Cappers, R. T. J., R. M. Bekker and J. E. A. Jans. 2006. Digital Seed Atlas of the Netherlands. Barkhuis Publishing, Eelde, Holland.

Chessel, D., A. B. Dufour and J. Thioulouse. 2004. The ade4 package - I: One-table methods. R news 4: 5-10.

de Crespin de Billy, V., S. Dolédec and D. Chessel. 2000 Biplot presentation of diet composition data: An alternative for fish stomach contents analysis. Journal of Fish Biology 56: 961-973.

Delany S. and D. Scott. 2006. Waterbird Population Estimates, 4th Edition. Wetlands International, Wageningen, Holland.

Duncan, P., A. J. M. Hewison, S. Houte, R. Rosoux, T. Tournebize, F. Dubs, F. Burel and V. Bretagnolle. 1999. Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. Journal of Applied Ecology 36: 11-23.

Efron, B. and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall, New York, New York.

Elphick C. S. and L. W. Oring. 1998. Winter management of Californian rice fields for waterbirds. Journal of Applied Ecology 35: 95-108.

Gibbs, J. P. 2000. Wetland destruction and degradation are generally linked with human activities. Conservation Biology 14: 314-317.

Green, A. J., J. Figuerola and M. I. Sanchez. 2002. Implications of waterbird ecology for the dispersal of aquatic organisms. Acta Oecologica 23: 177-189.

Grillas P. 1990. Distribution of submerged macrophytes in the Camargue in relation to environmental factors. Journal of Vegetation Science 1: 393-402.

Guillemain, M., H. Fritz, N. Guillon and G. Simon. 2002. Ecomorphology and coexistence in dabbling ducks: the role of lamellar density and body length in winter. Oikos 98: 547-551.

Heathwaite A. L. 2010. Multiple stressors on water availability at global to catchment scales: understanding human impact on nutrient cycles to protect water quality and water availability in the long term. Freshwater Biology 55: 241-257.

Kayser, Y., M. Gauthier-Clerc, A. Béchet, B. Poulin, G. Massez, Y. Chérain, J. Paoli, N. Sadoul, E. Vialet, G. Paulus, N. Vincent-Martin, P. Pilard and P. Isenmann. 2008. Compte-rendu ornithologique camarguais pour les années 2001-2006. Revue d'Ecologie (Terre Vie) 63: 299-349.

Kloskowski, J., A. J. Green, M. Polak, J. Bustamante and J. Krogulec. 2009. Complementary use of natural and artificial wetlands by waterbirds wintering in Doñana, south-west Spain. Aquatic Conservation: Marine and Freshwater Ecosystems 19: 815-826.

Lebart, L., A. Morineau and M. Piron. 2000. Statistique Exploratoire Multidimensionnelle, 3e Edition. Dunod, Paris, France.

Legendre, P. and L. Legendre. 1998. Numerical Ecology, 2nd English Edition. Elsevier, Amsterdam, Holland.

Marnotte, P., A. Carrara, E. Dominati and F. Girardot. 2006. Plantes des Rizières de Camargue. Cirad-CFR-PNRC, Montpellier, France.

Mateo, R., R. Guitart and A. J. Green. 2000. Determinants of lead shot, rice, and grit ingestion in ducks and coots. Journal of Wildlife Management 64: 939-947.

Molinier, R. and G. Talon. 1974. Documents pour inventaire des plantes vasculaires de la Camargue. Bulletin de la société d'Histoire Naturelle de Marseille 30: 5-110.

MWO (2012) Mediterranean Wetlands: Outlook. First Mediterranean Wetlands Observatory report - Technical report. Tour du Valat, France. Available at: http://medwetlands-obs.org, accessed May 2012.

Nummi, P. 1993. Food-niche relationships of sympatric Mallards and Green-winged Teals. Canadian Journal of Zoology 71: 49-55.

Perry, M. C., A. Welles-Berlin, D. M. Kidwell and P. C. Osenton. 2007. Temporal changes of populations and trophic relationships of wintering diving ducks. Waterbirds 30: 4-16.

Pirot, J. Y. 1981. Partage alimentaire et spatial des zones humides camarguaises par cinq espèces de canards en hivernage et en transit. Unpublished Ph.D. Thesis, Pierre et Marie Curie University, Paris, France.

Pöysä, H. 1987. Ecology of foraging behaviour in dabbling ducks (*Anas* sp.). Publications Sciences No. 10, University of Joensuu, Joensuu, Finland.

Rendòn, M. A., A. J. Green, E. Aquilera and P. Almaraz. 2008. Status, distribution and long-term changes in the waterbird community wintering in Doñana, south-west Spain. Biological Conservation 141: 371-1388.

Royal Botanic Garden Edinburgh, 2011. Flora Europaea. http://rbg-eb2.rbge.org.uk/FE/fe.html, accessed April 2011.

Storms, D., P. Aubry, J. L. Hammann, S. Saïd, H. Fritz, C. Saint-Andrieux and F. Klein. 2008. Seasonal variation in diet composition and similarity of sympatric Red Deer *Cervus elaphus* and Roe Deer *Capreolus capreolus*. Wildlife Biology 14: 237-250.

Swanson, G. A. and J. C. Bartonek. 1970. Bias associated with food analysis in gizzards of Blue-winged Teal. Journal of Wildlife Management 34: 739-746.

Tachet H., P. Richoux, M. Bournaud and P. Usseglio-Polera. 2000. Invertébrés d'Eau Douce : Systématique, Biologie, Ecologie. CNRS Editions, Paris, France.

Tamisier, A. 1971. Régime alimentaire des Sarcelles d'Hiver *Anas crecca* L. en Camargue. Alauda 39: 261-311.

Tamisier, A. 1990. Camargue, Milieu et Paysage : Evolution de 1942 à 1984. Arcane, Arles, France.

Tamisier, A., L. Allouche, F. Aubrey and O. Dehorter. 1995. Wintering strategies and breeding success: hypothesis for a trade-off in some waterfowl species. Wildfowl 46: 76-88.

Tamisier, A. and O. Dehorter. 1999. Camargue, Canards et Foulques. Fonctionnement et Devenir d'un Prestigieux Quartier d'Hiver. Centre Ornithologique du Gard, Nîmes, France.

Tamisier, A. and P. Grillas. 1994. A review of habitat changes in the Camargue an assessment of the effects of the loss of biological diversity on the wintering waterfowl community. Biological Conservation 70: 39-47.

Tourenq, C., R. E. Bennetts, H. Kowalski, E. Vialet, J. L. Lucchesi, Y. Kayser and P. Isenmann. 2001. Are ricefields a good alternative to natural marshes for waterbird communities in the Camargue, southern France? Biological Conservation 100: 335-343.

Table S1. Relative frequency of occurrence (*Ro*) and average relative dry weight (*Rw*) of food items present in gullet (both expressed in %), for Mallard (*n* = 119) and Teal (*n* = 302) (see text: 'Statistical analyses' section).

				Relative frequency of occurrence (%)		Average relative dry weight (%)	
			Abbreviation	Mallard	Teal	Mallard	Teal
Invertebrate							
1	Arachnida	Hydrachnellae	HYDRA		6.3		<0.1
2	Bryozoa	*Bryozoa* (statoblast)	BRY(S)	0.8	2.7	<0.1	<0.1
	Crustacea						
3	- Amphipoda	Corophiidae	CORO	1.7	1.3	0.1	<0.1
4		Gammaridae	GAMM		1.3		<0.1
5	- Cladocera	Cladocera (ephippia)	CLA(E)	0.8	12.6	<0.1	<0.1
6	- Isopoda	*Cyathura carinata*	CYACAR	5.0		1.5	
7		*Idotea* sp.	IDESP		0.3		<0.1
8		*Sphaeroma hockerii*	SPHHOO	1.7	0.7	1.5	0.3
9	Ostracoda	Ostracoda	OSTR	0.8	25.5	<0.1	1.4
	Insecta						
10	- Coleoptera	Dytiscidae (adult)	DYS(A)	0.8		<0.1	
11		Haliplidae (larvae)	HAL(L)		2.0		<0. 1
12		Hydrophilidae (larvae)	HYD(L)		7.6		0.3
13		Noteridae (larvae)	NOT(L)		0.7		<0.1
14		Other Coleoptera (adult and larvae)	COL(A, L)	6.7	9.6	0.1	0.2
15	- Diptera	Ceratopogonidae (larvae)	CER(L)		12.3		1.0
16		Chironomidae (larvae)	CHI(L)		17.6		1.8
17		Ephydridae (larvae)	EPH(L)	0.8	2.3	<0.1	0.3
18		Psychodidae (larvae)	PSY(L)		5.6		<0.1
19		Rhagionidae (larvae)	RHA(L)		0.7		<0.1
20		Stratiomyidae (larvae)	STR(L)		2.3		<0.1
21		Syrphidae (larvae)	SYR(L)		2.3		0.2
22		Tabanidae (larvae)	TAB(L)		1.0		<0.1
23		Tipulidae (larvae)	TIP(L)	0.8	0.3	<0.1	<0.1
24		Other Diptera (adult, nymph and larvae)	DIP(A, N, L)	1.7	12.9	<0.1	0.2
25	- Heteroptera	Corixidae (adult)	COR(A)	2.5	4.6	<0.1	<0.1
26		*Microvelia sp.* (adult)	MIC(A)		0.7		<0.1

[a]introduced plant species in France, according to Marnotte *et al.* (2006) and Flora Europaea (Royal Botanic Garden Edinburgh 2011)
[b]cultivated plant species

Table S1. (Continued) Relative frequency of occurrence (*Ro*) and average relative dry weight (*Rw*) of food items present in gullet (both expressed in %), for Mallard ($n = 119$) and Teal ($n = 302$) (see text: 'Statistical analyses' section).

				Relative frequency of occurrence (%)		Average relative dry weight (%)	
			Abbreviation	Mallard	Teal	Mallard	Teal
27		Naucoridae (adult)	NAUC(A)	0.8		<0.1	
28		Pleidae (adult)	PLE(A)		0.3		<0.1
29		Other Heteroptera (adult)	HETE(A)		0.3		<0.1
30	- Megaloptera	Megaloptera (larvae)	MEG(L)	0.8	0.3	<0.1	<0.1
31	- Odonata	Anisoptera (larvae)	ANI(L)		6.6		0.4
32		Zygoptera (larvae)	ZYG(L)		0.7		0.2
33		Other Odonata (larvae)	ODO(L)	7.6	7.0	<0.1	0.2
	Mollusca						
34	- Bilvalvia	*Cerastoderma edule*	CEREDU	0.8		0.8	
35	- Gasteropoda	Physidae	PHYS	25.2	34.8	0.2	5.1
36		Planorbidae	PLAN	31.1	34.8	1.1	3.8
37		Other Gasteropoda	GAST	8.4	7.6	0.9	<0.1
38	Platyhelminthes	Turbelaria	TURBE		4.6		<0.1
39	Protozoa	Foraminifera	FORA		0.3		<0.1
40	Undetermined	Undetermined invertebrate	INDI	1.7	3.6	<0.1	<0.1
Seeds							
41	Alismataceae	*Alisma plantago-aquatica*	ALIPLA		0.7		<0.1
42	Amaranthaceae	*Amaranthus deflexus* [a]	AMADEF		0.3		<0.1
43	Asteraceae	*Asteraceae* sp.	ASTESP	0.8		<0.1	
44	Callitrichaceae	*Callitriche* sp.	CALSP		0.3		<0.1
45	Caryophyllaceae	*Spergularia marina*	SPEMAR		0.3		<0.1
46	Characeae	*Chara* sp.	CHASP	4.2	36.4	<0.1	6.0
47	Chenopodiaceae	*Arthrocnemum glaucum*	ARTGLA		1.7		<0.1
48		*Atriplex prostrata*	ATRPRO	0.8		<0.1	
49		*Chenopodium* sp.	CHESP		0.7		<0.1
50		*Kochia hirsuta*	KOCHIR		0.3		<0.1
51		*Salicornia* sp.	SALSP	0.8	6.0	0.8	2.2
52		*Salsola soda*	SALSOD		1.0		<0.1
53		*Suaeda* sp.	SUASP	2.5	12.9	0.2	3.6
54	Compositae	*Helianthus annuus* [b]	HELANU	0.8		<0.1	
55		*Inula* sp.	INUSP		11.6		0.8
56	Cruciferae	*Brassica* sp.	BRASP		0.3		<0.1

[a]introduced plant species in France, according to Marnotte *et al.* (2006) and Flora Europaea (Royal Botanic Garden Edinburgh 2011)
[b]cultivated plant species

Table S1. (Continued) Relative frequency of occurrence (*Ro*) and average relative dry weight (*Rw*) of food items present in gullet (both expressed in %), for Mallard ($n = 119$) and Teal ($n = 302$) (see text: 'Statistical analyses' section).

				Relative frequency of occurrence (%)		Average relative dry weight (%)	
			Abbreviation	Mallard	Teal	Mallard	Teal
57	Cyperaceae	*Carex* sp.	CARSP	1.7		<0.1	
58		*Cyperus difformis*	CYPDIF		6.0		1.2
59		*Eleocharis palustris*	ELEPAL	6.7	19.9	0.4	2.9
60		*Eleocharis* sp.	ELESP		4.0		0.3
61		*Schoenoplectus mucronatus*	SCHMUC	10.9	13.9	0.3	1.0
62		*Scirpus maritimus*	SCIMAR	29.4	48.7	5.8	17.3
63		*Scirpus tabernaemontani*	SCITAB		0.3		<0.1
64		Other Cyperaceae sp.	CYPESP	0.8		<0.1	
65	Fabaceae	Fabaceae	FABSP		1.0		<0.1
66	Haloragaceae	*Myriophyllum spicatum*	MYRSPI	5.9	9.6	0.8	2.1
67	Juncaceae	*Juncus* sp.	JUNSP	0.8	9.6	<0.1	<0.1
68	Labiatae	*Lycopus europaeus*	LYCEUR	2.5	1.0	<0.1	<0.1
69	Leguminosae	*Trifolium* sp.	TRISP	0.8	2.3	<0.1	<0.1
70		*Vicia* sp.	VICSP		0.7		<0.1
71	Lemnaceae	*Lemna* sp.	LEMSP		0.3		<0.1
72	Malvaceae	*Althaea officinalis*	ALTOFF	0.8		<0.1	
73	Najadaceae	*Najas indica*	NAJIND	6.7	15.6	0.2	0.6
74		*Najas marina*	NAJMAR		0.3		<0.1
75		*Najas minor*	NAJMIN	4.2	18.2	<0.1	0.8
76		Other *Najas* sp.	NAJSP		2.0		<0.1
77	Onagraceae	*Ludwigia peploides* [a]	LUDPEP	4.2	13.3	0.7	1.9
78	Papaveraceae	*Papaver* sp.	PAPSP		0.3		<0.1
79	Poaceae	*Digitaria sanguinalis*	DIGSAN		0.7		<0.1
80		*Echinochloa* sp.	ECHSP	58.0	32.8	22.2	14.0
81		*Eleusine indica* [a]	ELUIND	0.8		<0.1	
82		*Eragrostis* sp.	ERASP		0.3		<0.1
83		*Festuca arundinacea*	FESARU	0.8	1.0	<0.1	<0.1
84		*Leersia oryzoides*	LEEORY		4.3		0.2
85		*Milium* sp. [b]	MILSP	2.5	4.6	0.4	1.9
86		*Oryza sativa* (and « receptacle ») [a, b]	ORYSAT(E)	53.8	28.8	35.1	8.5
87		*Panicum* sp.	PANSP		0.3		<0.1
88		*Paspalum distichum* [a]	PASDIS	2.5	10.6	<0.1	1.2
89		*Phragmites australis*	PHRAUS		17.6		0.8

[a]introduced plant species in France, according to Marnotte *et al.* (2006) and Flora Europaea (Royal Botanic Garden Edinburgh 2011)
[b]cultivated plant species

Table S1. (Continued) Relative frequency of occurrence (*Ro*) and average relative dry weight (*Rw*) of food items present in gullet (both expressed in %), for Mallard ($n = 119$) and Teal ($n = 302$) (see text: 'Statistical analyses' section).

				Relative frequency of occurrence (%)		Average relative dry weight (%)	
			Abbreviation	Mallard	Teal	Mallard	Teal
90		*Polypogon* sp.	POLYSP		1.7		0.3
91		*Setaria pumila*	SETPUM		0.3		<0.1
92		*Setaria verticillata*	SETVER	4.2	2.0	<0.1	<0.1
93		*Setaria viridis*	SETVIR	0.8	1.7	<0.1	<0.1
94		*Sorghum* sp. [a, b]	SORSP	2.5	2.7	0.7	1.1
95		*Triticum aestivum* [b]	TRIAES	7.6	5.0	5.4	2.8
96		*Zea mays* [a, b]	ZEAMAY	1.7		0.9	
97		Other Poaceae sp.	POASP	2.5	0.7	<0.1	<0.1
98	Polygonaceae	*Fallopia convolvulus*	FALCON	0.8	0.7	<0.1	<0.1
99		*Polygonum aviculare*	POLAVI		3.0		<0.1
100		*Polygonum lapathifolium*	POLLAP	8.4	9.0	<0.1	0.9
101		*Polygonum persicaria*	POLPER	4.2	5.0	0.1	0.3
102		Other *Polygonum* sp.	POLSP	7.6		1.7	
103		*Rumex* sp.	RUMSP	5.0	0.7	<0.1	<0.1
104	Pontederiaceae	*Heteranthera limosa* [a]	HETLIM		1.7		<0.1
105		*Heteranthera reniformis* [a]	HETREN	2.5	12.0	<0.1	0.4
106	Potamogetonaceae	*Potamogeton nodosus*	POTNOD	10.1	3.6	4.1	0.2
107		*Potamogeton pectinatus*	POTPEC	6.7	3.6	1.8	0.4
108		*Potamogeton pusillus*	POTPUS	24.4	41.4	7.2	7.9
109	Ranunculaceae	*Ranunculus* sp.	RANSP	0.8	12.9	<0.1	0.2
110	Rosaceae	*Rubus* sp.	RUBSP	2.5	4.0	0.3	0.6
111	Rubiaceae	*Galium* sp.	GALISP	0.8		<0.1	
112	Ruppiaceae	*Ruppia cirrhosa*	RUPCIR		0.7		<0.1
113		*Ruppia maritima*	RUPMAR	0.8	2.3	0.5	0.4
114	Solanaceae	*Solanum* sp.	SOLSP	0.8	1.0	<0.1	<0.1
115	Vitaceae	*Vitis vinifera* [b]	VITVIN	0.8		<0.1	
116	Zannichelliaceae	*Zannichellia* sp.	ZANSP	2.5	13.6	1.3	0.5
117	Zosteraceae	*Zostera noltii*	ZOSNOL	2.5	0.7	1.7	0.3
118	Undetermined	*Unidentified seed*	INDS	3.4	2.0	0.7	<0.1
			Vegetative part				
119	Potamogetonaceae	*Potamogeton pectinatus*	POTPEC(V)		0.7		<0.1
120	Undetermined	*Undetermined*	INDV	1.7	0.3	<0.1	<0.1

[a]introduced plant species in France, according to Marnotte *et al.* (2006) and Flora Europaea (Royal Botanic Garden Edinburgh 2011)
[b]cultivated plant species

Table S2. Mean and total dry weight for each food item consumed by Mallard and/or Teal (in mg)

Food item			Abbreviation	Mean dry weight	Total dry weight	
					Mallard	Teal
Invertebrate						
1	Arachnida	Hydrachnellae	HYDRA	0.05		4.60
2	Bryozoa Crustacea	*Bryozoa* (statoblast)	BRY(S)	0.10	0.10	10.00
3	- Amphipoda	Corophiidae	CORO	0.11	0.22	12.54
4		Gammaridae	GAMM	1.28		90.480
5	- Cladocera	Cladocera (ephippia)	CLA(E)	0.01	0.01	3.11
6	- Isopoda	*Cyathura carinata*	CYACAR	1.91	373.07	
7		*Idotea* sp.	IDESP	3.30		3.30
8		*Sphaeroma hockerii*	SPHHOO	4.00	296.22	644.56
9	Ostracoda Insecta	Ostracoda	OSTR	0.65	5.83	2,764.25
10	- Coleoptera	Dytiscidae (adult)	DYS(A)	1.32	1.32	
11		Haliplidae (larvae)	HAL(L)	0.50		4.50
12		Hydrophilidae (larvae)	HYD(L)	1.70		85.00
13		Noteridae (larvae)	NOT(L)	1.32		21.16
14		Other Coleoptera (adult and larvae)	COL(A, L)	2.68	493.00	117.50
15	- Diptera	Ceratopogonidae (larvae)	CER(L)	0.56		13,548.85
16		Chironomidae (larvae)	CHI(L)	0.29		1,997.23
17		Ephydridae (larvae)	EPH(L)	1.40	1.40	440.28
18		Psychodidae (larvae)	PSY(L)	0.30		44.70
19		Rhagionidae (larvae)	RHA(L)	0.50		32.50
20		Stratiomyidae (larvae)	STR(L)	0.87		20.01
21		Syrphidae (larvae)	SYR(L)	1.32		141.05
22		Tabanidae (larvae)	TAB(L)	0.45		4.05
23		Tipulidae (larvae) [a]	TIP(L)		13.50	16.5
24		Other Diptera (adult, nymph and larvae)	DIP(A, N, L)	0.71	15.82	67.30
25	- Heteroptera	Corixidae (adult)	COR(A)	0.82	20.50	39.98
26		*Microvelia sp.* (adult)	MIC(A)	0.02		1.37
27		Naucoridae (adult)	NAUC(A)	5.96	5.96	
28		Pleidae (adult)	PLE(A)	0.70		0.70
29		Other Heteroptera (adult)	HETE(A)	5.96		59.60

[a]No mean dry weight, each food item was weighted according to a broad food item size variation
[b]Data from Arzel *et al.* (2007

Table S2. (Continued) Mean and total dry weight for each food item consumed by Mallard and/or Teal (in mg)

Food item			Abbreviation	Mean dry weight	Total dry weight	
					Mallard	Teal
30	- Megaloptera	Megaloptera (larvae)	MEG(L)	0.50	2.5	7.50
31	- Odonata	Anisoptera (larvae)	ANI(L)	3.40		279.10
32		Zygoptera (larvae)	ZYG(L)	3.40		34.00
33		Other Odonata (larvae)	ODO(L)	3.40	98.60	752.90
	Mollusca					
34	- Bilvalvia	*Cerastoderma edule*	CEREDU	6.67	41.20	
35	- Gasteropoda	Physidae	PHYS	4.06	1,245.50	12,248.47
36		Planorbidae	PLAN	3.79	2,294.92	12,041.60
37		Other Gasteropoda	GAST	1.39	43.18	139.33
38	Platyhelminthes	Turbelaria	TURBE	1.01		35.65
39	Protozoa	Foraminifera	FORA	0.50		0.50
40	Undetermined	Undetermined invertebrate [a]	INDI		13.00	0.20
Seeds						
41	Alismataceae	*Alisma plantago-aquatica*	ALIPLA	0.30[b]		14.80
42	Amaranthaceae	*Amaranthus deflexus*	AMADEF	0.60		94.20
43	Asteraceae	*Asteraceae* sp.	ASTESP	<0.01	<0.01	
44	Callitrichaceae	*Callitriche* sp.	CALSP	0.05		0.15
45	Caryophyllaceae	*Spergularia marina*	SPEMAR	0.10		0.10
46	Characeae	*Chara* sp.	CHASP	0.03	0.27	1,8829.20
47	Chenopodiaceae	*Arthrocnemum glaucum*	ARTGLA	0.20		10.00
48		*Atriplex prostrata*	ATRPRO	0.41	0.41	
49		*Chenopodium* sp.	CHESP	0.24[b]		0.63
50		*Kochia hirsuta*	KOCHIR	0.41		0.82
51		*Salicornia* sp.	SALSP	0.14[b]	64.40	984.54
52		*Salsola soda*	SALSOD	0.20		32.64
53		*Suaeda* sp.	SUASP	0.57	106.79	134,290.33
54	Compositae	*Helianthus annuus*	HELANU	46.00	690.00	
55		*Inula* sp.	INUSP	0.09		229.41
56	Cruciferae	*Brassica* sp.	BRASP	1.09		38.12
57	Cyperaceae	*Carex* sp.	CARSP	1.17[b]		38.70

[a]No mean dry weight, each food item was weighted according to a broad food item size variation
[b]Data from Arzel *et al.* (2007

Table S2. (Continued) Mean and total dry weight for each food item consumed by Mallard and/or Teal (in mg)

Food item			Abbreviation	Mean dry weight	Total dry weight	
					Mallard	Teal
58		*Cyperus difformis*	CYPDIF	0.04		269.14
59		*Eleocharis palustris*	ELEPAL	0.57[b]	196.97	601.51
60		*Eleocharis* sp.	ELESP	0.27		143,604.69
61		*Schoenoplectus mucronatus*	SCHMUC	1.00	209.47	415.00
62		*Scirpus maritimus*	SCIMAR	3.29[b]	1,026.03	5,038.29
63		*Scirpus tabernaemontani*	SCITAB	0.30[b]		0.30
64		Other Cyperaceae sp.	CYPESP	0.80	0.80	
65	Fabaceae	Fabaceae[a]	FABSP			85.70
66	Haloragaceae	*Myriophyllum spicatum*	MYRSPI	0.97	20.39	62.08
67	Juncaceae	*Juncus* sp.	JUNSP	0.03[b]	0.03	89.88
68	Labiatae	*Lycopus europaeus*	LYCEUR	0.16[b]	7.41	33.81
69	Leguminosae	*Trifolium* sp.	TRISP	0.38	238.87	7.52
70		*Vicia* sp.	VICSP	2.10		4.20
71	Lemnaceae	*Lemna* sp.	LEMSP	0.20		56.00
72	Malvaceae	*Althaea officinalis*	ALTOFF	0.60	1.80	
73	Najadaceae	*Najas indica*	NAJIND	0.40	929.12	1,744.00
74		*Najas marina*	NAJMAR	7.79		7.79
75		*Najas minor*	NAJMIN	0.15	107.09	1,198.35
76		Other *Najas* sp.	NAJSP	0.03		2.37
77	Onagraceae	*Ludwigia peploides*	LUDPEP	0.45	119.71	690.61
78	Papaveraceae	*Papaver* sp.	PAPSP	0.05		0.05
79	Poaceae	*Digitaria sanguinalis*	DIGSAN	6.30		18.90
80		*Echinochloa* sp.	ECHSP	4.38	197,526.92	143,604.69
81		*Eleusine indica*	ELUIND	0.16	2.50	
82		*Eragrostis* sp.	ERASP	0.15		0.45
83		*Festuca arundinacea*	FESARU	1.55	4.65	7.75
84		*Leersia oryzoides*	LEEORY	0.89[b]		176.12
85		*Milium* sp.	MILSP	3.74[b]	2,054.25	18,305.24
86		*Oryza sativa*	ORYSAT (E)	15.00	273,855.00	59,520.90
87		*Panicum* sp.	PANSP	4.90		9.80

[a]No mean dry weight, each food item was weighted according to a broad food item size variation
[b]Data from Arzel *et al.* (2007

Table S2. (Continued) Mean and total dry weight for each food item consumed by Mallard and/or Teal (in mg)

Food item			Abbreviation	Mean dry weight	Total dry weight	
					Mallard	Teal
88		*Paspalum distichum*	PASDIS	0.47	54.17	3,537.22
89		*Phragmites australis*	PHRAUS	0.19		142.44
90		*Polypogon* sp.	POLYSP	0.06		360.64
91		*Setaria pumila*	SETPUM	2.59		2.59
92		*Setaria verticillata*	SETVER	0.71	35.96	98.70
93		*Setaria viridis*	SETVIR	1.60	22.40	30.40
94		*Sorghum* sp.	SORSP	25.16	8,278.63	17,614.21
95		*Triticum aestivum*	TRIAES	32.92	100,337.65	42,790.80
96		*Zea mays*	ZEAMAY	250.59 [b]	23,555.46	
97		Other Poaceae sp. [a]	POASP		252.29	<0.01
98	Polygonaceae	*Fallopia convolvulus*	FALCON	3.53	3.53	17.64
99		*Polygonum aviculare*	POLAVI	1.33 [b]		66.60
100		*Polygonum lapathifolium*	POLLAP	1.10 [b]	633.66	1,277.27
101		*Polygonum persicaria*	POLPER	1.14 [b]	226.98	140.74
102		Other *Polygonum* sp.	POLSP	1.21	6113.33	
103		*Rumex* sp.	RUMSP	1.27	16.47	2.53
104	Pontederiaceae	*Heteranthera limosa*	HETLIM	0.09		28.98
105		*Heteranthera reniformis*	HETREN	0.05	22.66	7,437.09
106	Potamogetonaceae	*Potamogeton nodosus*	POTNOD	2.71 [b]	191.71	148.83
107		*Potamogeton pectinatus*	POTPEC	3.20 [b]	114.09	83.85
108		*Potamogeton pusillus*	POTPUS	0.65	164.15	648.30
109	Ranunculaceae	*Ranunculus* sp.	RANSP	0.12	0.24	65.76
110	Rosaceae	*Rubus* sp.	RUBSP	1.81	77.87	99.41
111	Rubiaceae	*Galium* sp.	GALISP	2.25	4.50	
112	Ruppiaceae	*Ruppia cirrhosa*	RUPCIR	0.18		6.52
113		*Ruppia maritima*	RUPMAR	1.56	1.56	24.90
114	Solanaceae	*Solanum* sp.	SOLSP	0.62	3.72	65.72
115	Vitaceae	*Vitis vinifera*	VITVIN	15.80	15.80	
116	Zannichelliaceae	*Zannichellia* sp.	ZANSP	0.39	372.27	1,510.06
117	Zosteraceae	*Zostera noltii*	ZOSNOL	0.79	57.96	2.38

[a]No mean dry weight, each food item was weighted according to a broad food item size variation
[b]Data from Arzel *et al.* (2007

Table S2. (Continued) Mean and total dry weight for each food item consumed by Mallard and/or Teal (in mg)

Food item			Abbreviation	Mean dry weight	Total dry weight	
					Mallard	Teal
118	Undetermined	*Unidentified seed*[a]	INDS		144.25	31.86
Vegetative part						
119	Potamogetonaceae	*Potamogeton pectinatus*[a]	POTPEC(V)			181.44
120	Undetermined	*Undetermined*[a]	INDV		196.32	1,504.90

[a]No mean dry weight, each food item was weighted according to a broad food item size variation
[b]Data from Arzel *et al.* (2007