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Spatial and temporal variation in the diet of Marbled Teal *Marmaronetta angustirostris* in the western Mediterranean

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Capsule This globally threatened species is less dependent on invertebrates and more dependent on seeds than other ducks.

Aims To assess seasonal variation in Marbled Teal diet at two of the most important wetlands for the west Mediterranean population.

Methods Faecal samples from El Hothba, Morocco (19 in October, 28 in May) and Veta la Palma, Doñana (19 in August, five from July broods) were analysed. Gut contents of six birds from Veta la Palma (September–October) were analysed.

Results At El Hothba, small seeds (especially *Ruppia*) and green plant material (especially charophytes) were the dominant faecal components in May and October. The proportion of invertebrates did not change, but more Corixidae and less Chironomidae were consumed in May. At Veta la Palma, *Ruppia* seeds were dominant in August, but Ephydriidae, Chironomidae, Coleoptera and other insects were dominant in faeces from July broods. Significantly fewer Coleoptera but more Foraminifera were recorded in August. The overall proportion of invertebrates at El Hothba in May and October was higher than at Veta la Palma in August, but lower than in July broods. Corixidae were dominant in May, Ephydriidae in July broods, unidentified insects, Ostracoda and Foraminifera in August and Coleoptera in October. Gut contents from Veta la Palma confirmed the dominance of *Ruppia* seeds in the post-breeding diet.

Conclusion Marbled Teal differs in its ecology from the better-known north-temperate ducks. With the exception of ducklings, they are less dependent on invertebrates and rely on small seeds more than north-temperate ducks.

Although the Anatidae have been the subject of much research, most has concentrated on migratory species breeding in North America or northern Europe (Baldassarre & Bolen 1994, Kear in press). The findings may not be representative of the biology of little-known species found elsewhere, such as those breeding in the Mediterranean region.

The Marbled Teal *Marmaronetta angustirostris* is a globally threatened species (BirdLife International 2000) considered to be the most primitive member of the pochards Aythyini (Livezey 1996). Recently it has been shown to be well adapted to exploit the high spatial and temporal variation in habitat availability found in natural Mediterranean wetlands (Green 2000). It shows greater affinity with the dabbling ducks Anatini in habitat use and feeding behaviour than with the Aythyini (Green 1998a, Green & Hamzaoui 2000).

However, data on diet has so far been limited to a short study in Turkey, which found *Scirpus* seeds to be the major component, combined with a range of invertebrates (Green & Selva 2000).

Here we compare Marbled Teal diet in the breeding and post-breeding periods in Doñana in southwest Spain and Sidi Moussa-Qualidia in Morocco, two wetlands used by a common migratory population (Green 1993, Navarro & Robledano 1995). We consider how diet changed across the annual cycle in each wetland. We also investigate if the invertebrate component of the diet was more important during the breeding season, and the plant component more important during the non-breeding season, as with northern-temperate duck species (Krapu & Reinecke 1992). We also compare the diet at each wetland.

We use faecal analysis, a particularly useful method for studying the diet of threatened Anatidae (Razfindrahanta 1999, Green & Selva 2000). Faecal contents are

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biased towards harder, less digestible components of the diet (Swanson & Bartonek 1970; Sedinger 1986). Thus, we also use gut contents from smaller numbers of birds as a reference.

MATERIALS AND METHODS

Study area

Samples in Spain were collected from Veta la Palma (VLP), an extensive brackish fish farm of 3125 ha within Doñana Natural Park (36°57'N, 6°14'W), one of the two most important wetlands for Marbled Teal in Spain (Green & Navarro 1997, Green 2000). This site is used to culture estuarine fish such as European Seabass *Dicentrarchus labrax*, Flathead Mullet *Mugil cephalus* and Gilthead Seabream *Sparus auratus* as well as Atlantic Ditch Shrimp *Palaemonetes varians*. Submerged vegetation is dominated by Wigeongrass *Ruppia maritima* with small amounts of fennel pondweed *Potamogeton pectinatus*, and the shores and islands are covered with saltmarsh vegetation, especially *Arthrocnemum macrostachyum* and *Suaeda* spp.

Samples in Morocco were collected from Marais d'El Hotba-Wlad Salem (32°55'N 08°49'W; 'El Hotba' or EH) in the Sidi Moussa-Oualidia complex on the Atlantic coast. Submerged vegetation at this site is more varied than at VLP, being dominated by *Ruppia* but mixed with large areas of charophytes and *P. pectinatus*. There is abundant emergent vegetation (*Juncus*, *Scirpus*, *Phragmites* and *Typha*). The shorelines are dominated by *Salicornia* and other saltmarsh plants (see El Hamoumi *et al.* (2000) and Green *et al.* (2002a) for more details of EH).

Faecal samples

Fresh faecal samples were collected from islands where monospecific groups of Marbled Teal were observed resting. Before collection, birds were observed with a telescope, and a sketch was made using clumps of vegetation as reference points before wading to the islands to collect fresh faeces. We are confident that each sample came from a different individual, except samples collected from broods. At VLP, five faecal samples were collected from Marbled Teal broods, four on 26 July 1996 where two broods were resting (females with 7 and 8 class IIc ducklings) and one on 18 July 1997 from a female with 16 class IIa ducklings (see Green 1998b for age classes). Each sample may have contained faeces from several ducklings and/or the

adult female. On 22 and 27 August 1997, 19 faecal samples were collected from adults or juveniles (indistinguishable in field conditions). At EH, 19 faecal samples were collected on 24 October 1997 and 28 on 11 May 1999 (the height of the nesting period at this latitude, Green 1998b).

Faecal samples were stored individually in test tubes and air-dried. Prior to analysis they were rehydrated in water for 24 hours and then shaken using a Heidolph vortex to loosen them. They were then washed in a 0.04 mm sieve, preserved in 70% ethanol and examined with a 10–25× binocular microscope. Animal and plant food items were sorted and identified to the lowest possible taxonomic level using reference material of potential food items collected at the study sites with sweep nets, together with suitable keys (see Green & Selva 2000, Sánchez *et al.* 2000). The volume of the faecal sample represented by each food item was estimated using five categories of abundance: absent, < 10%, 10–50%, 51–90% and > 90% of total volume.

The minimum number of individual invertebrates consumed was established using head parts, elytra or other features (see Veltman *et al.* 1995, e.g. chironomid larvae heads survived digestion and were readily counted). Whole invertebrates from reference material were used to measure the average volume of each taxon. For organisms with volume > 0.01 ml, the volume of ten individuals selected at random was measured by displacement. Linear measurements of smaller organisms were taken, and their volume was estimated based on similar geometric forms (e.g. a sphere or a cylinder). Owing to their similar size and form, unidentified dipteran larvae or pupae were assigned the volume of chironomids. The volume of unidentified insects was estimated using the mean volume of insects in reference samples. These data were then used to estimate the original volume at ingestion of the invertebrates represented in the faeces (e.g. each chironomid head was assigned the volume of a whole larva).

Faecal samples with more than 10% green plant material were examined more closely using a 40–250× optical microscope. Epidermal structure was compared with microphotographs of various aquatic plant species in Spain (Amat & Soriguer 1982, Green & Selva 2000). In total, 22 samples were analysed in this way (at EH, five collected in October, 13 in May; at VLP, one collected from a July brood, three collected in August).

Gut samples

Six birds were found dead at VLP from 23 September to

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8 October 1997. Food items found in the gizzard and in oesophagus plus proventriculus were identified and stored in 70% ethanol. The actual volume of the contents of the gullet was measured as above.

Statistical analysis

For comparisons between sites and seasons, food items were combined into major categories. Full details of our identifications of plant and animal matter in Marbled Teal diet are available from the authors.

The percentage of individual samples in which each food item was recorded (i.e. the percentage occurrence) was calculated for faecal and gut samples for each site and season. Estimated volumes of invertebrates represented in the faeces, and actual volumetric measurements of all food items in the oesophagus plus proventriculus were expressed as the mean of individual volumetric percentages for each sample (aggregate percentage) and/or percentage of total volume combined for all samples (aggregate volume, Swanson *et al.* 1974).

Within each site, seasonal differences in percentage occurrence of different diet components in faeces were analysed with Mann–Whitney *U* tests using STATISTICA 5.5 (StatSoft Inc. 1999) procedures, assigning ranks to the five categories of abundance described above. Only those diet components found in at least 20% (at EH) or 50% (at VLP) of samples in one of the two seasons were tested statistically, and Bonferroni corrected. These different thresholds were applied because of the differences in sample sizes, and none of the components with lower percentage occurrences could have shown statistically significant differences.

The total estimated volume of invertebrates at ingestion as a percentage of the actual volume of a faecal sample was used as an index of the overall proportion of invertebrates in the diet. Differences in this index between sites and seasons were analysed using Kruskal–Wallis.

RESULTS

Faecal analysis: composition

At EH, faeces were dominated in volumetric terms by seeds and other plant matter, in October and May (Table 1). A number of invertebrates were recorded but in small quantities, and only Corixidae (in two May samples) and Chironomidae (in one October sample) made up $\geq 10\%$ of the volume of any sample. Seasonal

differences in composition were significant, with more *Ranunculus* seeds, unidentified seeds and Corixidae in May, and more *Ruppia* seeds, Chenopodiaceae seeds (mainly *Salicornia* spp.) and Chironomidae in October (Table 1). *Ruppia* seeds constituted $> 90\%$ of the volume of 12 (63%) of the October samples and two (7%) of the May samples. *Ranunculus* seeds constituted $> 90\%$ of six (21%) of the May samples.

At VLP, *Ruppia* seeds were dominant in August faeces, in which they constituted $> 90\%$ of the volume of 16 (84%) of the samples. A wide variety of invertebrates were recorded in August, but only in small quantities (Table 1). In contrast, invertebrates represented the major proportion of the volume of faecal samples from July broods (Table 1), with Chironomidae, Ephydriidae or Coleoptera constituting $> 50\%$ of the volume of four of the five samples and $> 90\%$ of three of them. Seasonal differences in composition were significant, with more *Ruppia* seeds and Foraminifera in August, and more Coleoptera in July broods (Table 1). Overall, more types of seeds and other plant matter were recorded at EH, and more categories of invertebrates at VLP (Table 1).

In the 22 faecal samples in which green plant material was studied with a microscope, three had no epidermal remains, making identification impossible. In the other 19, the presence of charophytes was confirmed in 13 (four at EH in October, nine at EH in May, Table 1). In four samples at EH in May there was epidermis similar to *Potamogeton*, *Zannichellia* or *Ranunculus*. There were six samples at EH (one in October, five in May) with epidermis that may have been Chenopodiaceae. There was no evidence of the presence of *Ruppia*.

Invertebrates in faeces: extrapolating to volume at ingestion

There were major differences in the relative importance of invertebrate groups between wetlands and seasons (Fig. 1): Chironomidae were most important in October (at EH) and in July broods (at VLP). Corixidae were most important in May (at EH). Ephydriidae were only important in July broods (at VLP), and Ostracoda and Foraminifera only in August (at VLP). Coleoptera were important in all four sets of samples, and unidentified insects in all except July broods (Fig. 1).

There was a highly significant difference between the four sets of samples in the proportion of invertebrates in faeces (Kruskal–Wallis test, $H = 32.5$, $df = 3$, $P <$

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Table 1. Contents of Marbled Teal faeces from El Hotba (EH, Morocco) and Veta la Palma (VLP, Spain), showing the percentage occurrence of each food item (PO) and the percentage of samples in which each item represented at least 10% of sample volume ($V \geq 10$).

	El Hotba				U	Veta la Palma				
	May (n = 28)		October (n = 19)			July broods (n = 5)		August (n = 19)		U
	PO	$V \geq 10$	PO	$V \geq 10$		PO	$V \geq 10$	PO	$V \geq 10$	
Green plant material	100	46.43	100	26.32	197	100	20	100	15.79	44
Charophyta ¹	32.14	32.14	21.05	21.05	–	0	0	0	0	–
Seeds	96.43	71.43	100	94.74	–	80	20	100	100	–
<i>Ruppia</i>	78.57	35.71	100	94.74	62**	80	20	100	100	0**
<i>Ranunculus</i>	42.86	32.14	0	0	152*	0	0	0	0	–
Chenopodiaceae	7.14	0	52.6	0	145**	20	0	0	0	–
<i>Zannichellia</i>	7.14	0	0	0	–	0	0	0	0	–
<i>Potamogeton</i>	3.57	0	0	0	–	0	0	0	0	–
Charophyta oospores	67.86	17.86	73.68	21.05	251.5	0	0	15.79	0	–
Unidentified	53.57	10.71	10.53	0	148.5*	40	0	26.32	0	–
Invertebrates	100	7.14	100	5.26	–	100	100	84.21	0	–
Chironomidae L/P	3.57	0	42.11	5.26	163*	80	40	0	0	9.5
Ephyridae P	10.71	0	5.26	0	–	80	60	0	0	9.5
Other Diptera L/P	10.71	0	0	0	–	0	0	5.26	0	–
Coleoptera A	57.14	0	63.16	0	250	100	20	15.79	0	6*
Corixidae	85.71	7.14	10.53	0	64**	100	0	21.05	0	10
Homoptera	3.57	0	0	0	–	0	0	5.26	0	–
Hymenoptera	3.57	0	5.26	0	–	20	0	0	0	–
Unidentified Insecta	7.5	0	68.42	0	248.5	60	0	31.58	0	34
Corixidae eggs	71.43	0	63.16	0	244	80	0	5.26	0	12
Acarina	0	0	5.26	0	–	0	0	0	0	–
Araneida	0	0	10.53	0	–	60	0	0	0	19
Isopoda	0	0	0	0	–	0	0	5.26	0	–
Palaemonidae	0	0	0	0	–	0	0	5.26	0	–
<i>Daphnia</i> ephippia	32.14	0	42.11	0	239.5	0	0	0	0	–
Ostracoda	0	0	10.53	0	–	0	0	57.89	0	20
Gastropoda	0	0	5.26	0	–	0	0	5.26	0	–
Bryozoan statoblasts	0	0	0	0	–	0	0	5.26	0	–
Foraminifera	0	0	0	0	–	0	0	84.21	0	7.5*
Unidentified invertebrates	0	0	0	0	–	0	0	5.26	0	–
Unidentified eggs	10.71	0	0	0	–	0	0	5.26	0	–
Vertebrates										
Bone fragment	0	0	0	0	–	0	0	5.26	0	–

L, larvae; P, pupae; A, adults. Seasonal differences were tested within each site using Mann–Whitney *U* tests. * $P < 0.05$, ** $P < 0.01$ after Bonferroni correction. ¹Subset of green plant material, PO likely to be underestimated since only samples where $V \geq 10$ for green plant material were studied microscopically (see Methods).

0.0001). Post-hoc Mann–Whitney *U* tests showed that, at EH, the difference in the total estimated volume of invertebrates at ingestion as a percentage of the actual volume of a faecal sample between October (range = 0.01–466.4, median = 4.0) and May (range = 1.2–62.3, median = 5.1) was not significant ($P = 0.38$). In contrast, at VLP July broods (range = 37.3–748.1, median = 100.1) had significantly more invertebrates than in August (range = 0.02–5.6, median = 0.59, $P < 0.001$). Furthermore, the proportion of invertebrates at EH in both October and May was higher than at VLP in August ($P < 0.001$) and lower than at VLP in July broods ($P < 0.001$).

Gut content analysis

At VLP, the gut contents of birds collected in September and October were generally similar to the composition of faeces from August, and confirm the dominance of *Ruppia* seeds in the post-breeding diet (Table 2). The data for aggregate percentage and aggregate volume may have been biased towards harder material such as seeds and gastropods owing to the method of collection and the low volume of the ingesta in some oesophagi and proventriculi (range 0.003–1.13 ml). However, in the bird with highest ingesta volume, *Ruppia* seeds represented 92.6%.

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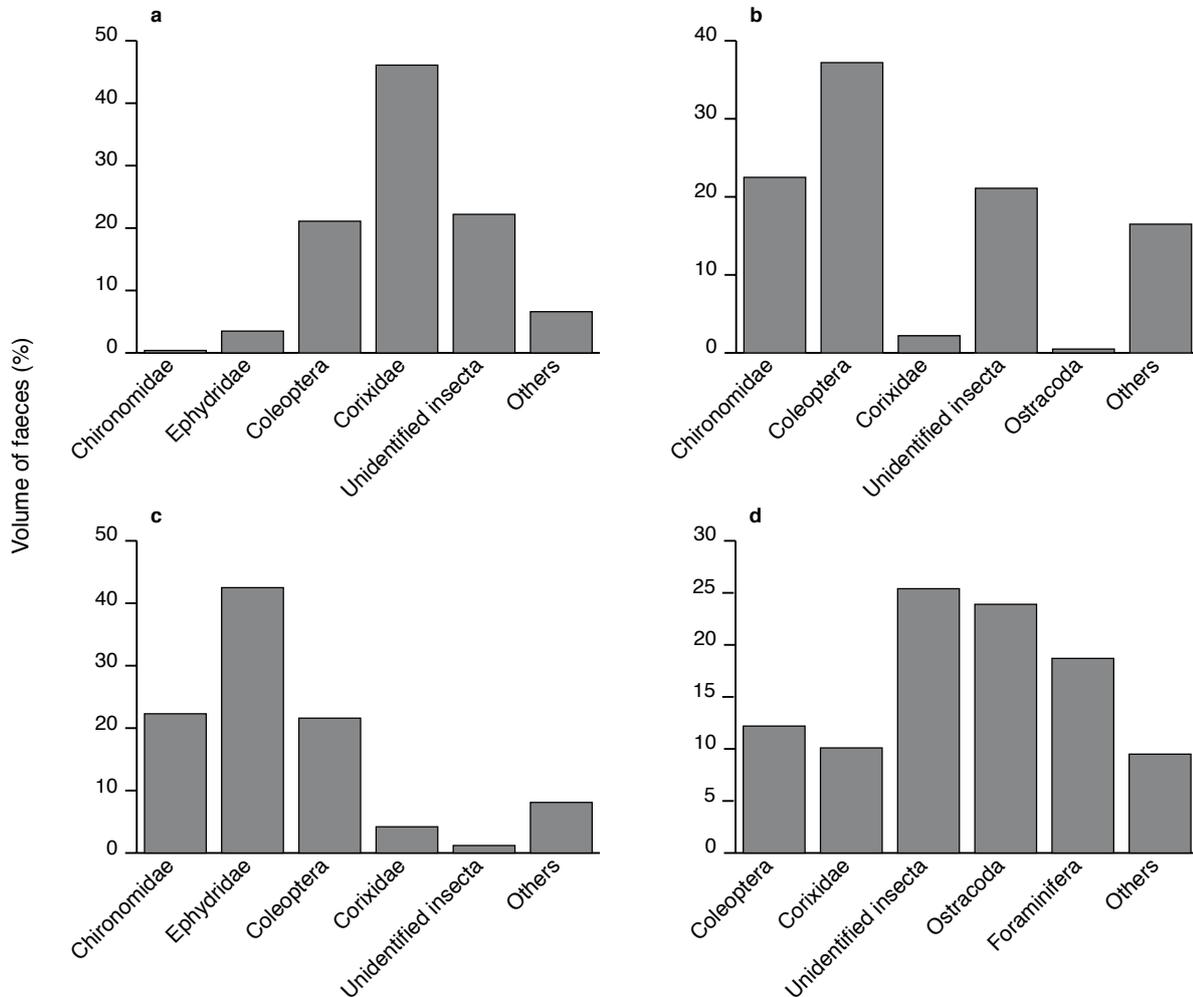


Figure 1. Mean of volumetric percentages (aggregate percentage) of different invertebrate groups in faecal samples from El Hothba (EH) in May (a) and October (b) and Veta la Palma (VLP) July broods (c) and in August (d). Estimated volumes upon ingestion of each group were extrapolated from observed volumes to compensate for differing digestability (see Methods). Groups shown are those used in Table 1. All groups that represented 10% or more of the aggregate percentage in at least one of the four sets of samples are shown separately, all others are pooled. Ephyrididae are not shown for EH October, but were present at 0.02%.

DISCUSSION

This is the most detailed study of Marbled Teal diet to date. Despite the biases inherent in faecal analysis, it allows a good approximation of diet composition and is particularly useful when comparing diet of the same species at different times and places, or different species at a given time and place (Green & Selva 2000). We suggest that the dominance of seeds amongst faecal contents in samples from VLP in August and EH in October, and the dominance of seeds combined with green plant material at EH in May, are not due to digestive biases. Firstly, even when extrapolating from invertebrate fragments to original volume at ingestion,

the ratio of invertebrate volume (and biomass) to that of plant material remained low in May, August and October. Secondly, despite any biases, insects dominated the faeces of July broods at VLP. Thirdly, the gut contents from VLP in September/October were similar to the faeces from August confirming that *Ruppia* seeds were dominant in the post-breeding diet.

Our results at VLP show that Marbled Teal broods had a diet particularly rich in invertebrate protein vital for duckling growth, as found in many other ducks (Krapu & Reinecke 1992). By late August (when adults had probably completed post-breeding wing moults), the diet was based on *Ruppia* seeds and partic-

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Table 2. Gut contents of Marbled Teal collected from Veta la Palma (VLP, Spain) in September and October, showing percentage occurrence (PO, combined for oesophagus, proventriculus and gizzard), mean of volumetric percentages in the oesophagus + proventriculus (aggregate percentage) and percentage of total volume in the oesophagus + proventriculus (aggregate volume). Values in parentheses = *n* (two of the six teal had empty gullets). L, larvae; P, pupae; A, adults.

	PO (6)	Aggreg. % (4)	Aggreg. Vol. (4)
Green plant material	100	18.61	0.46
Chlorophyta	17	0.49	0.004
Seeds	100	66.32	91.91
<i>Ruppia</i>	100	56.49	91.75
Unidentified	33	9.81	0.091
Charophyta oospores	17	0.02	0.07
Invertebrates	33	14.58	7.61
Chironomidae L/P	17	0.01	0.05
Coleoptera A	17	0.004	0.01
Corixidae	17	1.84	0.07
Gastropoda	33	11.82	4.78
Ostracoda	33	0.81	2.61
<i>Daphnia</i> ephippia	17	0.001	0.004
Diptera eggs	17	–	–
Unidentified Insecta	17	0.004	0.01
Unidentified inverts.	17	0.001	0.005
Foraminifera	33	0.09	0.07
Polychaeta	17	0.001	0.005

ularly low in invertebrates. At EH the proportion of invertebrates was intermediate, with no difference between May and October. In contrast, Aythyini and Anatini ducks breeding in north-temperate regions typically feed more on invertebrates during the pre-breeding and nesting periods than in the non-breeding season, partly due to the protein requirements for egg-laying (Krapu & Reinecke 1992, Baldassarre & Bolen 1994). However, exceptions to this generalization can be found in the literature (Green *et al.* 2002b), and the few studies on ducks breeding outside the temperate zone suggest they can be much less dependent on invertebrates (Kingsford 1989, Petrie 1996). Low invertebrate content in the diet may partially explain why Marbled Teal commence egg-laying later than sympatric duck species (Green *et al.* 1999). In Alicante, Spain, Marbled Teal gut contents show no increase in invertebrates during the breeding season (C. Fuentes, M.I. Sánchez, N. Selva & A.J. Green unpubl. data). However, although Marbled Teal can breed in their first year of age (Kear in press), many of our samples may be from non-breeders.

It is unclear to what extent the differences in diet recorded between sites and seasons reflect differences in prey selection, or changes in availability of potential food items. Like other ducks, Marbled Teal respond to

changes in availability and this explains why post-breeding birds fed largely on *Ruppia* seeds at EH or VLP but largely on *Scirpus* seeds at other wetlands in Turkey (Green & Selva 2000) or in Alicante, Spain (C. Fuentes, M.I. Sánchez, N. Selva & A.J. Green unpubl. data), where these similarly sized seeds are more abundant. The changes in abundance of different seeds in diet at EH between May and October are probably related to differing fruiting times of food plants. *Ranunculus* seeds were only consumed in May, and *Ranunculus* spp. produce fruits early in the season (Volder *et al.* 1997). In contrast, *Ruppia* and *Salicornia* seeds (consumed more in October) are produced in late summer and autumn (Verhoeven 1979, Van Eerden 1984).

When sampling faeces at EH, we also collected diurnal flock-scan data that showed how changes in diet coincided with changes in feeding methods, with a switch to shallower feeding depths in May. While 36.6% of feeding birds (*n* = 186) scanned in October were upending, 58.1% neck-dipping and 4.8% bill-dipping, in May 98.1% of teal (*n* = 52) were neck-dipping (see Green 1998a for details of each behaviour and corresponding depth). These data suggest that seeds were taken mainly from the sediments, and were relatively depleted in shallower, more profitable feeding areas by October (Guillemain & Fritz in press). There was also an apparent switch from feeding on nektonic corixids in May to benthic chironomid larvae in October. However, our study confounds different seasons with different years, and some invertebrates and plants are likely to have been far more abundant in some years than others. For example, chironomidae show major annual variation in abundance (Gardarsson & Einarsson 1994).

Our study and that of Green & Selva (2000) in Turkey suggest that Marbled Teal are heavily reliant on small seeds (especially *Ruppia* and *Scirpus*) and consume less green plant material than many other Aythyini and Anatini (the lack of *Ruppia* leaves and stems in diet in this study, in spite of their abundance, is consistent with the lack of *P. pectinatus* in Turkey). However, charophytes were important in the diet at EH. Relatively large seeds such as *P. pectinatus* and relatively large invertebrates such as shrimps seem to be avoided by Marbled Teal (this study and Green & Selva 2000).

It is possible that we overlooked some invertebrates consumed by birds because they left no visible trace in faeces (e.g. if small benthic planarians present at VLP were consumed), but we doubt that such items would have been abundant. *Daphnia* spp. and other zooplankton are readily digested and may have been over-

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looked as a component of the diet in faecal analysis. The *Daphnia ephippia* (resting eggs) recorded at EH may have been ingested while inside reproductive individuals, or else from sediments or while floating at the surface. Marbled Teal have been observed filtering *Daphnia magna* at other wetlands (C. Fuentes unpubl. data), and they have sufficiently fine lamellae in their bill (similar to those of Eurasian Teal *Anas crecca*) to enable them to filter larger zooplankton (Nummi 1993, Green & Selva 2000).

The relative abundance of benthic ostracods and foraminiferans in faeces from VLP in August suggests they may have been taken incidentally while birds were feeding on *Ruppia* seeds in the sediments. Foraminiferans (a marine group of protozoans, Barnes 1980) are present in the benthic sediments at VLP owing to the inflow of water from the Guadalquivir estuary.

The Marbled Teal is a Mediterranean species differing considerably in both evolutionary and ecological terms from the north-temperate ducks that have been the focus of much research (Livezey 1996, Green 2000). More research is required to establish to what extent the diet observed in this study is typical across the range of this threatened species. We expect considerable variation, since major concentrations have been observed at fresher Moroccan wetlands in which *Ruppia* is absent or rare (e.g. Dayet 'Awa or Barrage Al Massira, Green *et al.* 2002a). However, these sites have an abundance of other plants producing similar-sized seeds (e.g. *Polygonum amphibium* and *Potamogeton pusillus*) that may be important food items.

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