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Average mass of seeds encountered by foraging dabbling ducks in western Europe

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Many dabbling ducks *Anas* spp. are largely granivorous, consuming a variety of seeds chiefly from aquatic plants. To assess the relative value and carrying capacity of wetlands for dabbling ducks, species-specific information about seed mass is needed, but it is still largely missing or scattered in the literature. By combining weights of seeds collected in the field with a literature review, we provide a reference table for seed mass of 200 western European plant taxa frequently encountered by foraging dabbling ducks. Seeds collected in the field were sampled in microhabitats and at depths at which ducks were observed to forage, and study sites represent wintering, staging as well as breeding areas within a flyway in western Europe. When combined with calorimetric data, the present reference table will aid managers and scientists in assessing the importance of seed food resources at different sites and during different parts of the annual cycle.

Key words: core sample, dabbling ducks, seed mass, waterfowl, wetland

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Many species of dabbling ducks *Anas* spp. are largely granivorous in fall and winter, and partly so in spring and summer (e.g. Cramp & Simmons 1977, Glutz von Blotzheim 1990, Del Hoyo et al. 1992). Throughout a waterfowl flyway, the relative value and the carrying capacity of wetlands may thus largely depend on the seed stock available at different sites. However, no studies have so far provided comprehensive information about the amount of energy available to seed-eating ducks. Most likely this is due to the problems of comparing different types of data. Wetland seed stocks are generally expressed as number per area unit (Grillas et al. 1993, Bonis & Lepart 1994, Thompson et al. 1997), though a few studies provide information about the actual mass of seeds per area (e.g. Tamisier 1971a, Baldassarre & Bolen 1984, Clark et al. 1986). In studies of duck diet, however, abundance of seeds in the digestive tract is expressed as either aggregate % volume, aggregate % dry weight or as frequency of occurrence (e.g. Olney 1963, Olney 1964, Tamisier 1971b, Danell & Sjöberg 1980, Pehrsson 1979, Thomas 1982, Schricke 1983, Miller 1987). Sampling also causes problems; even in large seed samples, some plant species turn out to be fairly rare, resulting in a sample size too small to calculate a reliable mean mass for the plant species in question. In effect, it is far easier and more time efficient to count seeds visually in mud samples under a microscope in the laboratory than to collect seeds in the field individually with pliers for subsequent weighing.

Thus, a serious shortcoming of expressing food abundance as the number of seeds per area unit is

that this information cannot be directly translated into a measure of energy available to foraging ducks (expressed in kcal or kJ per mass unit dry weight; e.g. Sugden 1973, Paulus 1982, Baldassarre & Bolen 1984, Hoffman & Bookhout 1985, Van Eerden & Munsterman 1997). Knowing species-specific seed mass is thus crucial to bridge the gap between the present data sets, but such information is largely unavailable for European species or, if existing, is scattered in the literature. The aim of our paper is to fill this gap by providing a reference table of average mass of natural wetland seeds and crops potentially ingested by dabbling ducks in western Europe. We both present primary data and provide a compilation of values found in the literature.

Study area and methods

We sampled seeds in France and Sweden as integrated parts of research projects addressing feeding ecology, time use and microhabitat use of dabbling ducks (Schricke 1983, Guillemain et al. 2002, Legagneux 2002, Arzel et al. 2003). The French samples were obtained from five distinct geographical areas: the Camargue, close to Arles on the Mediterranean coast (43°40'N, 4°37'E), during October 2003 - July 2004, in October 2004 and in February 2005; the Brenne area, close to Mézières en Brenne (46°49'N, 1°12'E), during August - September 2002 and 2003; the Baie de Seine, close to Le Havre (49°29'N, 0°07'E), in February and March 2003 and 2004; the Baie du Mont Saint Michel

(48°38'N, 1°30'W) during August - September 1980-1982; the Marais de Rochefort (45°53'N, 01°05'W) during October 1996 - March 1997, in October 1999 and in August 2004. The Swedish samples were collected from three distinct geographical areas: on the island of Öland in the Baltic Sea (56°42'N, 16°42'E) in April 2003; in the vicinity of Kristianstad in the very south of Sweden (56°01'N, 14°09'E) in April 2003 and 2004; and near Umeå in north-central Sweden (63°49'N, 20°16'E) during May - July in 2003 and 2004. Sampled habitats included temporary wetlands, coastal meadows, coastal lagoons, fluvial meadows and lakes ranging from eutrophic to oligotrophic. As part of more extensive research programmes, the foraging behaviour of dabbling ducks was studied regularly at most sites as part of the daily routine before we sampled food resources. Therefore, samples were generally taken in macro- and microhabitats where dabbling ducks were actually seen foraging, or where faeces, footprints and feathers indicated recent foraging activity. In this way, we ensured that samples were representative of seeds encountered by foraging dabbling ducks. Although we did not strive to include every occurring seed-producing plant species, we assumed that the long sampling periods, the wide geographical coverage and the variety of habitats included provided a very good representation of important forage seeds available to ducks at wintering, spring staging and breeding sites within this flyway.

Core sample volume varied among sites (within 63-407 cm³) as did the number of samples (10-30/site/sampling day), but as we did not intend to analyse seed abundance, we do not consider these methodological differences a problem. Seeds in the Baie du Mont Saint Michel, in the Brenne area and in western France in August 2004 were hand-picked directly from plants instead of core-sampled. Seeds were hand-sorted under a binocular microscope after the cores of plant litter and sediment had been sieved. Sieve mesh size was 300 µm; hence, all seeds down to this size were considered as long as they were not empty or otherwise obviously unviable. Indeed, the minimum size of food items that a duck can effectively capture is determined by the spaces between the bill lamellae, ranging from 0.3 mm in teal *Anas crecca* and northern shoveler *Anas clypeata* to 1 mm in mallard *Anas platyrhynchos*, with all other European dabbling duck species falling between these values (Thomas 1982, Nudds & Bowlby 1984, Tolkamp 1993). We

used Beijerinck (1947), Berggren (1969, 1981), Anderberg (1994) and the internet resources <http://www.bioimages.org.uk/> and http://www.dijon.inra.fr/malherbo/hyppa/hyppa-f/hyppa_f.htm to identify seeds. We also used the nomenclature adopted by these sources. We oven-dried seeds at 60°C until desiccation, i.e. for at least 24 hours (Thomas 1982). In cases where seeds of the same plant species were collected at more than one location (e.g. by Matthieu Guillemain in Camargue, Pierre Legagneux in Brenne and Céline Arzel in Sweden), average seed mass was calculated based on the total sample (i.e. samples from different sites were pooled).

Results and discussion

We provide data on average seed mass of 200 taxa (of which 168 were identified to species and 32 to genus) belonging to 43 families (Table 1). *Chara* oogons were included because they sometimes constitute a large share of the diet of granivorous dabbling ducks (Tamisier 1971a, Campredon et al. 1982). Seed mass differed markedly among species, ranging from 0.0077 mg in whorled leaf water milfoil *Myriophyllum verticillatum* to 21.90 mg in caley pea *Lathyrus hirsutus* (disregarding acorns and heavy seeds from agricultural plants such as maize *Zea mays* and barley *Hordeum vulgare*).

The sample size of some species is rather small (e.g. < 5 seeds in annual seablite *Suaeda maritima*, grey sedge *Carex divulsa*, field bindweed *Convolvulus arvensis* and water mannagrass *Glyceria fluitans*), but considering the very small amount of data available elsewhere, the information provided here still makes a valuable contribution. Intraspecific variation in seed mass can be substantial (Susko & Lovett-Doust 2000), and mass data based on small sample sizes must be used with caution. We hope to see future additions to our present reference table, especially more data for species from which limited samples were obtained, and studies addressing intraspecific spatio-temporal variation in seed size are needed.

All seeds treated here were collected in duck foraging habitats, and some of the plant species indeed form the bulk of the diet of dabbling ducks in western Europe, at least seasonally (e.g. Mazzuchi 1971, Tamisier 1971a, Pehrsson 1979). To truly understand the importance of seeds as food for dabbling ducks, information about the energy content of representative species is also needed. Calorimetric data are available for some species (e.g. Hoffman &

Bookhout 1985, Joyner et al. 1987, Loesch & Kaminski 1989) and are being developed for others (P. Legagneux, unpubl. data). Combined with calorimetric data, our present reference table will make

up a helpful tool for managers and scientists in assessing the relative value of foraging sites and estimating the carrying capacity of natural wetlands.

Table 1. Average mass of plant seeds collected in France and Sweden, supplied by available values from literature. N denotes the number of seeds weighed in the present study, and all values are given in mg dry weight. The literature from which data were available include: ^a Grime et al. 1988, ^b Tamisier 1971a, ^c Grillas et al. 1993, ^d Van Eerden & Munsterman 1997, ^e Campredon et al. 1982, ^f Kantrud 1996, ^g Van Wijk 1988 (average value for *P. pectinatus* was computed from this source), ^h Rhazi et al. 2004, and ⁱ Maranon & Grubb 1993.

Family	Species	N	Seed mass	Literature
Alismaceae	<i>Alisma plantago-aquatica</i>	157	0.296	0.270 ^a , 0.210 ^b
	<i>Baldelia ranunculoides</i>	62	0.177	
Apiacea	<i>Cicuta virosa</i>	35	0.691	
	<i>Conium maculatum</i>	3	0.400	
	<i>Oenanthe fistulosa</i>	9	0.511	
	<i>Oenanthe</i> sp.	1	16.200	
Araceae	<i>Calla palustris</i>	16	1.513	
Asteraceae	<i>Bidens tripartitus</i>	22	1.491	
	<i>Bidens</i> sp.	25	0.576	
	<i>Cirsium arvense</i>			1.170 ^a
	<i>C. palustre</i>			2.000 ^a
	<i>C. vulgare</i>			2.640 ^a
	<i>Cirsium</i> sp.	4	1.125	
	<i>Gnaphalium uliginosum</i>	195	0.011	
	<i>Senecio jacobea</i>			0.050 ^a
	<i>Senecio</i> sp.			0.400 ^b
	<i>Taraxacum officinalis</i>	20	0.545	
	<i>Taraxacum</i> sp.			0.640 ^a
Betulaceae	<i>Alnus glutinosa</i>	30	0.610	1.300 ^a
	<i>Betula alba</i>	100	0.117	
	<i>B. pendula</i>	100	0.117	
	<i>Betula</i> sp.			0.120 ^a
Brassicaceae	<i>Brassica napus</i>	2376	3.623	
	<i>Brassica</i> sp.	50	1.332	
	<i>Rorippa amphibia</i>	16	0.038	
	<i>R. palustris</i>	47	0.659	0.070 ^a
	<i>Rorippa</i> sp.	13	0.062	
Callitrichaceae	<i>Callitriche palustris</i>	234	0.059	
	<i>C. platycarpa</i>	58	0.031	
	<i>C. truncata</i>			0,065 ^c
	<i>C. vulgaris</i>		0.090	
	<i>Callitriche</i> sp.	45	0.082	
Caprifoliaceae	<i>Sambucus nigra</i>	6	2.250	3.400 ^a
Caryophyllaceae	<i>Cerastium fontanum</i>		0.160	
	<i>Lychnis flos-cuculi</i>	35	0.070	
	<i>Spergula arvensis</i>	49	0.040	
	<i>Spergularia marina</i>	614	0.054	
	<i>S. maritime</i>			0.087 ^d
	<i>S. media</i>	23	0.074	
	<i>S. salina</i>			0.053 ^d
Ceratophyllaceae	<i>Ceratophyllum demersum</i>	4	9.050	
	<i>Ceratophyllum</i> sp.	10	9.350	
Characeae	<i>Chara</i> (small)			0.030 ^e
	<i>Chara</i> (medium size)	626	0.137	0.150 ^d
	<i>Chara</i> (Öland, Sweden)	511	0.010	
	<i>Chara</i> (Donaña, Spain)			0.025 ^e

Table 1; continued...

Family	Species	N	Seed mass	Literature
Chenopodiaceae	<i>Arthrocnemum glaucum</i>			0.200 ^b
	<i>Atriplex hastata</i>	605	0.499	0.860 ^a ; 0.390 ^b
	<i>A. hortensis</i>	300	2.156	
	<i>Atriplex</i> sp.	2569	0.574	
	<i>Chenopodium album</i>	67	0.525	1.350 ^a
	<i>C. glaucum</i>	630	0.126	
	<i>C. polyspermum</i>			
	<i>C. rubrum</i>	12	0.142	
	<i>Chenopodium</i> sp.	129	0.238	
	<i>Obione portulacoides</i>			0.300 ^b
	<i>Salicornia dolichostachya</i>			0.161 ^d
	<i>S. fruticosa</i>			2.800 ^b
	<i>S. herbacea</i>			0.050 ^b
	<i>Sarcocornia</i> sp.	250	0.139	
	<i>Suaeda fruticosa</i>			0.330 ^b
		<i>S. maritima</i>	1	0.8000
Convolvulaceae	<i>Convolvulus arvensis</i>	3	2.267	
Cyperaceae	<i>Carex acuta</i>	15	0.993	
	<i>C. bohemica</i>	7	0.443	
	<i>C. canescens</i>	43	0.286	
	<i>C. disticha</i>	87	0.403	
	<i>C. divulsa</i>	1	1.200	
	<i>C. elata</i>	21	0.767	
	<i>C. extensa</i>	11	1.991	
	<i>C. hirta</i>	9	1.322	
	<i>C. limosa</i>	74	1.391	
	<i>C. otrubae</i>	64	0.586	
	<i>C. pallescens</i>	25	0.852	
	<i>C. panicea</i>	4	0.775	
	<i>C. pseudocyperus</i>	120	0.510	
	<i>C. riparia</i>	47	1.166	
	<i>C. rostrata</i>	600	0.746	
	<i>C. serotina</i>	121	0.042	
	<i>C. vesicaria</i>	13	1.508	
	<i>C. vulpina</i>	1	0.250	
	<i>Carex</i> sp.	17	1.171	
	<i>Cladium mariscus</i>	30	1.327	
	<i>Cyperus</i> sp.			0.006 ^b
	<i>Eleocharis acicularis</i>	100	0.041	
	<i>E. palustris</i>	1114	0.568	0.960 ^a ; 0.540 ^b
	<i>E. uniglumis</i>	494	0.453	
	<i>Scirpus lacustris</i>	905	1.601	1.660 ^b ; 1.191 ^d
	<i>S. litoralis</i>			0.740 ^b
<i>S. maritimus</i>	412	3.293	2.350 ^b ; 5.600 ^f	
<i>S. mucronatus</i>			1.000 ^b	
<i>S. tabernaemontani</i>	434	0.298		
	<i>Scirpus</i> sp.	14	1.029	
Fabaceae	<i>Lathyrus hirsutus</i>	5	21.900	
	<i>Lotus corniculatus</i>	8	1.138	1.670 ^a
	<i>L. uliginosus</i>	21	0.552	0.400 ^a
	<i>Medicago lupulina</i>	5	1.740	2.010 ^a
	<i>Trifolium arvense</i>	27	0.333	
	<i>T. pratense</i>	110	1.419	1.350 ^a
	<i>T. repens</i>	1026	0.503	
	<i>Trifolium</i> sp.	153	0.376	
		<i>Vicia cracca</i>		

Table 1; continued...

Family	Species	N	Seed mass	Literature
Fagacea	<i>Quercus</i> sp.	33	3323.291	
Haloragaceae	<i>Myriophyllum alternifolius</i>			0.492 ^c
	<i>M. spicatum</i>	167	0.747	
	<i>M. verticillatum</i>	13	0.008	
	<i>Myriophyllum</i> sp.			0.970 ^b
Hippuridacea	<i>Hippuris vulgaris</i>	51	0.478	
Iridacea	<i>Iris pseudacorus</i>	1	17.300	
Isoetacea	<i>Isoetes setacea</i>			0.098 ^h
Juncacea	<i>J. bufonius</i>	1000	0.021	0.020 ^a
	<i>J. bulbosus</i>		0.022	0.030 ^a
	<i>J. compressus</i>	665	0.022	
	<i>J. effusus</i>			0.011 ^d
	<i>J. gerardii</i>	15	0.035	
	<i>Juncus</i> sp.	4624	0.025	
Lamiaceae	<i>Prunella vulgaris</i>	13	0.215	
	<i>Lycopus europaeus</i>	16	0.161	
	<i>Mentha aquatica</i>	18	0.094	0.140 ^a
Lemnaceae	<i>Lemna minor</i>	4	0.200	0.600 ^a
Lythraceae	<i>Lythrum salicaria</i>	4	0.063	
	<i>Peplis portula</i>	408	0.016	
Menyanthaceae	<i>Menyanthes trifoliata</i>	7	1.771	
Naiadaceae	<i>Naias marina</i>	3260	7.790	
Nymphaeaceae	<i>Nymphaea alba</i>	57	12.528	
Oenotheraceae	<i>Epilobium hirsutum</i>	68	0.062	0.050 ^a
	<i>E. palustre</i>	33	0.118	0.040 ^a
	<i>E. parviflorum</i>			0.110 ^a
	<i>Epilobium</i> sp.	23	0.057	
Plantaginaceae	<i>Plantago lanceolata</i>	102	1.879	
	<i>P. major</i>	185	0.154	0.240 ^a
Poaceae	<i>Agrostis stolonifera</i>	17	0.277	
	<i>Alopecurus geniculatus</i>	10	0.120	0.380 ^a
	<i>Alopecurus</i> sp.	5	0.140	
	<i>Avena barbata</i>			2,630 ⁱ
	<i>Baldingera arundinacea</i>	2	0.330	
	<i>Bromus hordeaceus</i>			0.910 ⁱ
	<i>Bromus</i> sp.	205	2.519	
	<i>Crypsis aculeata</i>	100	0.371	
	<i>Cynosorus cristatus</i>			0.700 ^a
	<i>Echinochloa crus-galli</i>	13,240	1.446	
	<i>Glyceria fluitans</i>	3	0.500	1.200 ^a
	<i>G. maxima</i>			0.740 ^a
	<i>Glyceria</i> sp.	303	2.424	
	<i>Hordeum vulgare</i>	91	38.7835	
	<i>Leerzia oryzoides</i>	60	0.885	
	<i>Milium</i> sp.	229	3.735	
	<i>Oryza sativa</i>			15.000 ^b
<i>Panicum crus-galli</i>			4.000 ^b	
<i>Paspalum distichum</i>			0.470 ^b	
<i>Poaceae</i> sp.	37	0.063		
<i>Triticum vulgare</i>	2138	32.916		
<i>Zea mays</i>	89	250.590		

Table 1; continued...

Family	Species	N	Seed mass	Literature
Polygonaceae	<i>Polygonum amphibium</i>	44	2.389	
	<i>P. aviculare</i>	388	1.332	1.450 ^a
	<i>P. hydropiper</i>	83	1.474	
	<i>P. lapathifolium</i>	2326	1.103	
	<i>P. minus</i>	40	0.798	
	<i>P. persicaria</i>	721	1.135	2.120 ^a
	<i>Rumex acetosa</i>	10	0.670	
	<i>R. conglomeratus</i>	517	0.740	
	<i>R. crispus</i>	5	0.680	1.330 ^a
	<i>R. hydrolapathum</i>	14	1.971	
	<i>R. maritimus</i>	170	0.154	0.517 ^d
	<i>R. palustris</i>	50	0.718	
Potamogetonaceae	<i>Potamogeton berchtoldi</i>			0.650 ^b
	<i>P. gramineus</i>	262	2.446	
	<i>P. natans</i>	1052	2.316	
	<i>P. nodosus</i>	18	2.706	
	<i>P. obtusifolius</i>	86	2.594	
	<i>P. pectinatus</i>	66	3.199	3.870 ^b , 4.624 ^e
	<i>Potamogeton</i> sp.	5	2.100	
Primulaceae	<i>Anagallis arvensis</i>	43	0.147	0.400 ^a
	<i>Lysimachia vulgaris</i>	70	0.164	
Ranunculaceae	<i>Ranunculus baudotii</i>			0.178 ^c
	<i>R. flammula</i>	30	0.550	0.370 ^a
	<i>R. peltatus</i>	19	0.247	0.250 ^a
	<i>R. repens</i>	6	2.550	2.320 ^a
	<i>R. sardous</i>	162	1.112	
	<i>R. sceleratus</i>	142	0.241	
	<i>R. trichophyllus</i>	878	0.301	
	<i>Ranunculus</i> sp.	100	0.171	0.120 ^b
Rosaceae	<i>Filipendula ulmaria</i>			0.990 ^a
	<i>Potentilla anserina</i>	3	0.433	
	<i>P. palustris</i>	253	0.440	
	<i>Potentilla</i> sp.	131	0.049	
	<i>Rubus fruticosus</i>			2.490 ^a
	<i>Rubus</i> sp.	1253	2.115	
Rubiaceae	<i>Galium palustre</i>	52	0.462	0.910 ^a
Ruppiales	<i>Ruppia cirrhosa</i>	47	0.181	
	<i>R. maritima</i>	273	1.556	2.000 ^b
Salsolaceae	<i>Kochia hirsuta</i>			0.410 ^b
Scrophulariaceae	<i>Veronica anagallis-</i>	18	0.033	
Sparganiaceae	<i>Sparganium angustifolium</i>	92	8.128	
	<i>S. emersum</i>	9	2.111	
	<i>Sparganium</i> sp.	225	2.309	
Urticaceae	<i>Urtica dioica</i>	79	0.118	0.190 ^a
Vitaceae	<i>Vitis vinifera</i>	26	15.804	
Zanichelliaceae	<i>Zanichellia palustris</i>	156	0.279	130 ^e
	<i>Zanichellia</i> sp.			0.130 ^b , 0.146 ^c

Another step in assessing the carrying capacity of a wetland is to define the true metabolisable energy (TME) of different food items (Sherfy 1999). This is because the digestibility may differ between seeds from different species, and calorimetric data may

not always reflect what birds can actually metabolise (Sherfy 1999). Although TME values are essential in the end, individual seed mass remains useful for calculating and predicting TME (Sibbald 1980, Sherfy 1999).

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References

- Anderberg, A-L. 1994: Atlas of seeds and small fruits of Northwest-European plant species (Sweden, Norway, Denmark, East Fennoscandia, Iceland). Part 4, Resedaceae-Umbelliferae. - Swedish Museum of Natural History, Stockholm, 281 pp.
- Arzel, C., Guillemain, M. & Elmberg, J. 2003: Individual strategies of dabbling ducks: a circum-annual perspective. - 3rd North American Duck Symposium, Sacramento, California, Abstracts, 102 pp.
- Baldassare, G.A. & Bolen, E.G. 1984: Field-feeding ecology of waterfowl wintering on the Southern High Plains of Texas. - *Journal of Wildlife Management* 48: 63-71.
- Beijerinck, W. 1947: *Zaadenatlas der Nederlandsche flora: Ten behoeve de botanie, palaeontologie, bodemcultuur en Warenkennis*. - Veenman & Zonen, Wageningen, 316 pp. (In Dutch).
- Berggren, G. 1969: Atlas of seeds and small fruits of Northwest-European plant species with morphological descriptions. Part 2, Cyperaceae. - Swedish Museum of Natural History, Stockholm, 107 pp.
- Berggren, G. 1981: Atlas of seeds and small fruits of Northwest-European plant species with morphological descriptions. Part 3, Salicaceae-Cruciferae. - Swedish Museum of Natural History, Stockholm, 261 pp.
- Bonis, A. & Lepart, J. 1994: Vertical structure of seed banks and the impact of depth of burial on recruitment in two temporary marshes. - *Vegetatio* 112: 127-139.
- Campredon, S., Campredon, P., Pirot, J-Y. & Tamisier, A. 1982: Manuel d'analyse des contenus stomacaux de canards et de foulques. - In: ONC. (Ed.), Paris, 88 pp. (In French).
- Clark, R.G., Greenwood, H. & Sugden, L.G. 1986: Estimation of grain wasted by field-feeding ducks in Saskatchewan. - *Journal of Wildlife Management* 50: 184-189.
- Cramp, S. & Simmons, K.E.L. (Eds.), *The birds of the Western Palearctic*. Vol. 1: Ostrich to ducks. - Oxford University Press, Oxford, London, New York, 722 pp.
- Danell, K. & Sjöberg, K. 1980: Foods of widgeon, teal, mallard, and pintail during the summer in a northern Swedish lake. - *Swedish wildlife research (Viltrevy)* 11: 141-167.
- Del Hoyo, J., Elliott, A. & Sargatal, J. 1992: *Handbook of the Birds of the World*. Vol. 1. - Lynx Edicions, Barcelona, Spain, 696 pp.
- Glutz von Blotzheim, U. (Ed) 1990. *Handbuch der Vögel Mitteleuropas*. Band 2 Anseriformes, 2nd edition. - Aula-verlag, Wiesbaden, 535 pp. (In German).
- Grillas, P., Garcia-Murillo, P., Geertz-Hansen, O., Marbá, N., Montes, C., Duarte, C.M., Tan Ham, L. & Grossman, A. 1993: Submerged macrophyte seed bank in a Mediterranean temporary marsh: abundance and relationship with established vegetation. - *Oecologia* 94: 1-6.
- Grime, J.P., Hodgson, J.G. & Hunt, R. 1988: Comparative plant ecology: a functional approach to common British species. - Unwin Hyman, London, 742 pp.
- Guillemain, M., Leray, G., Caizergues, A. & Schricke, V. 2002: Dynamique de la population de la sarcelle d'hiver (*Anas crecca*). (In French with an English summary: Population dynamics of teal (*Anas crecca*)) - ONCFS rapport scientifique 2002, pp. 55-58.
- Hoffman, R.D. & Bookhout, T.A. 1985: Metabolizable energy of seeds consumed by ducks in Lake Erie marshes. - *Transactions of the North American Wildlife and Natural Resources Conference* 50: 557-565.
- Joyner, D.E., Jacobson, B.N. & Arthur, R.D. 1987: Nutritional characteristics of grains fed to Canada Geese. - *Wildfowl* 38: 89-93.
- Kantrud, H.A. 1996: The alkali (*Scirpus maritimus* L.) and saltmarsh (*S. robustus* Pursh) bulrushes: a literature review. - U.S. National Biological Service Information and Technology Report 6, 77 pp.
- Legagneux, P. 2002: Utilisation spatio-temporelle de la Brenne par les canards de surface en hivernage. - M.Sc. thesis, Pierre and Marie Curie University, Paris 6, 30 pp. (In French).
- Loesch, C.R. & Kaminski, R.M. 1989: Winter body-weight patterns of female mallards fed agricultural seeds. - *Journal of Wildlife Management* 53: 1081-1087.
- Maranon, T. & Grubb, P.J. 1993: Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. - *Functional Ecology* 7: 591-599.
- Mazzucchi, L. 1971: Beitrag zur Nahrungsökologie der Umgebung von Bern überwinternder Krickenten *Anas crecca* L. - *Der Ornithologische Beobachter* 68: 161-178. (In German).
- Miller, M.R. 1987: Fall and winter foods of northern pintails in the Sacramento valley, California. - *Journal of Wildlife Management* 51: 405-414.

- Nudds, T.D. & Bowlby, J.N. 1984: Predator-prey size relationships in North American dabbling ducks. - *Canadian Journal of Zoology* 62: 2002-2008.
- Olney, P.J.S. 1963: The food and feeding habits of teal *Anas crecca crecca* L. - *Proceedings of the Zoological Society of London* 140: 169-210.
- Olney, P.J.S. 1964: The food of mallard *Anas platyrhynchos platyrhynchos* collected from coastal and estuarine areas. - *Proceedings of the Zoological Society of London* 142: 397-418.
- Paulus, S.L. 1982: Feeding ecology of gadwalls in Louisiana in winter. - *Journal of Wildlife Management* 46: 71-79.
- Pehrsson, O. 1979: Skötsel av våtmarker för fröproduktion. - PM 1244. Statens Naturvårdsverk, Stockholm, Sweden, 84 pp. (In Swedish).
- Rhazi, M., Grillas, P., Charpentier, A. & Médail, F. 2004: Experimental management of Mediterranean temporary pools for conservation of the rare quillwort *Isoetes setacea*. - *Biological Conservation* 118: 675-684.
- Schricke, V. 1983: Distribution spatio-temporelle des populations d'Anatidés en transit et en hivernage en baie du Mont Saint-Michel, en relation avec les activités humaines. - PhD. thesis, Université Rennes, 299 pp. (In French).
- Sherfy, M.H. 1999: Nutritional value and management of waterfowl and shorebird foods in Atlantic coastal moist-soil impoundments. - PhD. thesis, Faculty of the Virginia Polytechnic Institute and State University, 265 pp + annexes.
- Sibbald, I.R. 1980: Metabolizable energy in poultry nutrition. - *BioScience* 30: 736-741.
- Sugden, L.G. 1973: Feeding ecology of pintail, gadwall, American widgeon and lesser scaup ducklings. - *Canadian Wildlife Service, Report Series* 24, 45 pp.
- Susko, D.J. & Lovett-Doust, L. 2000: Patterns of seed mass variation and their effects on seedling traits in *Allaria petiolata* (Brassicaceae). - *American Journal of Botany* 87(1): 56-66.
- Tamisier, A. 1971a: Les biomasses de nourriture disponible pour les sarcelles d'hiver *Anas crecca crecca* en Camargue. - *Revue d'écologie (Terre & Vie)* 25: 344-377. (In French with an English summary).
- Tamisier, A. 1971b: Régime alimentaire des sarcelles d'hiver *Anas crecca* L. en Camargue. (In French with an English summary: The diet of teal ducks, *Anas crecca*, in the Carmargue region). - *Alauda* 39: 261-311.
- Thomas, G.J. 1982: Autumn and winter feeding ecology of waterfowl at the Ouse Washes, England. - *Journal of Zoology (London)* 197: 131-172.
- Thompson, K., Bakker, J.P. & Bekker, R.M. 1997: The soil seed banks of north west Europe: methodology, density and longevity. - Cambridge University Press, 276 pp.
- Tolkamp, C.R. 1993: Filter-feeding efficiencies of dabbling ducks (*Anas* spp.) in relation to microhabitat use and lamellar spacing. - M.Sc. thesis, University of Guelph, Ontario, Canada, 43 pp.
- Van Eerden, M. & Munsterman, M.J. 1997: Patch use upon touch: filter-feeding European Teal *Anas crecca* have environmentally and socially determined foraging goals. - In: Van Eerden, M.R. (Ed.); *Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands*. PhD thesis, State University of Groningen, The Netherlands, pp. 165-185.
- Van Wijk, R.J. 1988: Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life-cycle under field conditions. - *Aquatic Botany* 31: 211-258.