

REVIEW

Is diet segregation between dabbling ducks due to food partitioning? A review of seasonal patterns in the Western Palearctic

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Abstract

Within the paradigm of resource-limited competition-structured communities, dabbling ducks (*Anas* spp.) have been used as a textbook example of how morphological differences, notably bill lamellar density and body length, may allow sympatric species to partition food and hence coexist. We reviewed all accessible diet studies from the Western Palearctic for three closely related dabbling duck species, mallard (*Anas platyrhynchos*), pintail (*A. acuta*) and teal (*A. crecca*), and present a comprehensive list of the food items (invertebrates, seeds, vegetative parts of plants) ingested. To assess the circumannual perspective of niche separation, we evaluated size distribution of ingested seeds among seasons and duck species. There was a significant difference among duck species in mean size and mass of ingested seeds, as well as in diet composition, with the largest seeds consumed by the largest species (mallard) with the coarsest bill filter apparatus (lamellae), and the smallest seeds by the smallest species (teal) with the finest bill lamellae. However, no effect of season was found, suggesting consistent diet segregation among species throughout the annual cycle of ducks and over large geographical areas. We argue that the patterns of food size separation between the three species are compatible with the idea of coexistence under interspecific competition.

Introduction

Wetlands often support several closely related species utilizing similar food resources (Weller, 1999). Ducks (*Anatidae*), especially dabbling ducks (*Anas* spp.), have often been presented as textbook examples of how subtle morphological differences among sympatric species may facilitate niche separation in terms of diet, and hence reduce interspecific competition (Lack, 1971, 1974) and structure communities (Schoener, 1983). In general terms, all *Anas* species are morphologically similar, having a flat bill lined with lamellae on the inside. The latter are used to filter water or mud in order to retain food particles. The size of ingested grit, invertebrates and seeds vary with the spacing (coarseness) of the bill lamellae, which in turn correlates largely with body size. Generally speaking, small

duck species, such as teal (*A. crecca*), have finer lamellae and are able to eat smaller food items than larger ducks with coarser lamellae, such as mallards (*A. platyrhynchos*) (Nudds & Wickett, 1994). The existence and causality behind food segregation in dabbling ducks has long been debated; some workers have stressed the importance of differences in bill lamellar density (Thomas, 1982; Nudds & Bowlby, 1984; Nudds, Sjöberg & Lundberg, 1994), others in body length (Thomas, 1982; Pöysä, 1983; Pöysä *et al.*, 1994; Green, 1998), foraging behaviour (Pöysä, 1987; Nummi, 1993), or the effect of habitat structure (Nudds *et al.*, 2000). However, the relative importance of these factors remains far from understood. Previous studies have demonstrated food partitioning between dabbling duck species in situations where competition is more likely (e.g. when duck density is high on wintering grounds;

Guillemain *et al.*, 2002). A broader assessment of diet segregation is much called for in order to understand general patterns of differences in resource use between these closely related species.

The aim of this article was to review diet studies concerning three closely related dabbling ducks (mallard, teal and pintail *A. acuta*) throughout their annual cycle in the Western Palearctic. In general, these species have very similar resource and habitat requirements. They have similar annual diet shifts, generally being granivores in autumn and winter and relying more on invertebrates in spring and summer (Cramp & Simmons, 1977; Krapu & Reinecke, 1992; Arzel *et al.*, 2009). Moreover, they span most of the range in crucial morphological characteristics among dabbling ducks, such as body mass (means of 1.07 kg, 0.84 kg and 0.32 kg for mallard, pintail and teal, respectively, Cramp & Simmons, 1977) and lamellar density (means of 8.0 lamellae/cm, 10.4 lamellae/cm and 15.0 lamellae/cm of bill for mallard, pintail and teal, respectively, Nudds *et al.*, 1994). Because they are widespread, common and also popular game species they are relatively well-studied, and there is a fair number of diet studies based on shot birds (e.g. Cramp & Simmons, 1977; Del Hoyo, Elliot & Sargatal, 1992; Kear, 2005).

We first compiled the available literature to make a comprehensive review of the food taxa (invertebrates, seeds and vegetative parts) utilized by each species. We then tested for differences in composition and size of ingested seeds by duck species and season. We predicted that the mean size of seeds should be positively related to species-specific density of bill lamellae.

Methods

Diet review

After reviewing 59 studies dealing with the diet of mallard, pintail and/or teal in the Western Palearctic from 1897 to 2007 (Table 1), we compiled all food items recorded in these studies (453 plant and 294 animal taxa; Supporting Information Tables S1 and S2). These studies are independent, that is in the cases where studies were based on at least partially the same data; we report here only the first one. Flora Europaea (Royal Botanic Garden Edinburgh, 2011) was used to name and group plant taxa, and the Animal Diversity Web (University of Michigan Museum of Zoology, 2011) to name and group animal taxa.

Statistical analysis

Statistical analyses were subsequently based on seed data only. Based on the literature, it is indeed difficult to study invertebrate size in the context of diet segregation, as most invertebrates reported in this review have been classified by very broad taxonomic groupings, and because individual size can range from half a millimetre to several centimetres within a given group. Moreover, several of the reviewed diet

studies relied on duck stomach content, and such data are known to give biased results, under-representing quickly digestible soft food items (Swanson & Bartonek, 1970). Our statistical analyses concern data from adult birds only, as our prediction was based on bill morphology and hence, may not be appropriate for ducklings. Duckling diet data from three studies (Lees & Street, 1974; Bengtson, 1975; Danell & Sjöberg, 1980) were therefore removed from the dataset prior to analyses.

Three measurements of seed size were used in the analyses: mass ($N = 1668$, $N_{\text{studies}} = 39$), length and width ($N = 2151$, $N_{\text{studies}} = 41$) (Supporting Information Table S3). The sample size (n) provided above for each dependent variable corresponds to the sum of the number of seeds species eaten by at least one duck species in one place in one diet study. A study may therefore provide several data to the analysis if it deals with several species and/or seasons. Consequently, a given seed species was therefore used four times in the dataset either if it was recorded in four different studies or if it was recorded in four seasons in one single study.

Seed mass data came from Arzel *et al.* (2007) complemented by measurements we took for some species for which data were not previously available and for seed species that we had in our own reference collection. In the latter cases, we measured seed mass by weighing a given number of seeds (most often 30) per species, oven-dried beforehand at 60°C for 24 h, and then divided the reading by the number of seeds, following the procedure in Arzel *et al.* (2007). Seed length and width measurements are from Cappers, Bekker & Jans (2006), who collected these after placing seeds under a digital camera. Seed species that we did not have in our reference collection and for which length and width were not measured by Cappers *et al.* (2006) were not taken into account in the analyses. Size measurements were used as a dependent variable in a second step of the analysis (see later). Thus, 41 diet studies were included in the statistical analysis (35 concerning mallard, 17 for pintail and 28 for teal), of which 33 were carried out in autumn, 29 in winter, 9 in spring and 15 in summer (some studies covered several seasons). Each diet study had the same 'weight' in the analyses, regardless of the number of ducks included, because sample size (i.e. number of birds for which diet was analysed) was not always provided by the authors.

We first carried out an analysis of similarity (ANOSIM) to examine differences in diet composition of the three duck species. ANOSIM is a non-parametric test designed to evaluate spatial differences and temporal changes in the assemblages of species (Clarke, 1993; Chapman & Underwood, 1999). ANOSIM procedures are based on the comparisons of intra- and inter-group distances calculated as average ranked values (using the Bray–Curtis measures of dissimilarity) in abundances and types of organisms among replicates between samples. We represented abundance as the sum of the number of seeds species eaten by at least one duck species in one place in one diet study, recorded as many times as the number of different duck species and/or different seasons were quoted (same procedure as for the sample size of seed measurements, see earlier). The ANOSIM statistic R is based on the

Table 1 Location, duck species and season for each study in the literature review

Code	Reference	Location	Duck species	Season
1	Bengtson (1975) ^a	Iceland	M, P, T	Su
2	Birger (1907)	Sweden	M, T	A
3	Brouwer (1980)	France	T	A, W
4	Campbell (1947)	United Kingdom	M, T	A, W
5	Curtet <i>et al.</i> (2004)	France	M, T	A, W
6	Danell & Sjöberg (1980) ^a	Sweden	M, P, T	Su
7	de Vries (1939)	The Netherlands	M, P, T	A, W
8	Dementiev & Gladkov (1967)	Russia	M, P, T	A, W, Sp, Su
9	Figuerola, Green & Santamaría (2003)	Spain	M, P, T	W
10	Gaevskaya (1966)	Russia	M, P, T	A, W, Sp, Su
11	Gardarsson & Einarsson (2002)	Iceland	M, P, T	Su
12	Gavrín (1964)	Russia	P	A, W, Sp
13	Goyon Demonteil (2004)	France	M, P, T	A, W
14	Green & Selva (2000)	Turkey	M	Su
15	Guillemain & Fritz (2002); Guillemain <i>et al.</i> (unpubl. data)	France	M, P, T	A, W
16	Gwiazda (1996)	Poland	M	Unknown
17	Hartman (1985)	Sweden	M	Su
18	Hesselman (1897)	Sweden	M, T	Unknown
19	Höhn (1948)	United Kingdom	M	A, W, Sp, Su
20	Holmboe (1900)	Norway	T	Unknown
21	Kiss, Rekasi & Sterbetz (1984)	Rumania	M	A
22	Lanchon-Aubrais (1992)	France	M	A, W, Su
23	Lees & Street (1974) ^a	United Kingdom	M	Sp, Su
24	Legagneux <i>et al.</i> (unpub. data)	France	M, P, T	A, W
25	Llorente, Ruiz & Serra-Cobo (1987)	Spain	T	A
26	Madsen (1988)	Denmark	T	A
27	Mazzucchi (1971)	Switzerland	T	W
28	Molodovsky (1971)	Russia	T	A, Sp, Su
29	Mouronval <i>et al.</i> (2007)	France	M, T	A, W
30	Nummi (1990)	Finland	M, T	A
31	Nummi (1993)	Finland	M, T	A
32	Nummi & Väänänen (2001)	Finland	M, P, T	A
33	Olney (1962)	United Kingdom	M	A, W
34	Olney (1963)	United Kingdom	T	A, W
35	Olney (1964)	United Kingdom	M	A, W
36	Olney (1965)	United Kingdom	M, P, T	A, W, Sp, Su
37	Pirkola (1966)	Finland	M	Su
38	Pirot (1981)	France	M, P, T	A, W
39	Rodrigues & Ferreira (1993)	Portugal	M	A
40	Rodrigues, Figueiredo & Fabiao (2002)	Portugal	M	A
41	Sanchez <i>et al.</i> (unpub. data)	Spain	M, P, T	A, W
42	Schricke (1983)	France	T ^b	A, W
43	Schricke <i>et al.</i> (unpub. data)	France	M, P, T ^c	A, W
44	Sotnikov (1999)	Russia	T	Sp, Su
45	Spärck (1947)	Denmark	M, P, T	A, W, Sp, Su
46	Srebrodol'skaya & Pavluk (1976)	Russia	M	Unknown
47	Staav (1976)	Sweden	M	A, Su
48	Sterbertz (1967)	Hungary	M	A, W, Sp, Su
49	Sterbertz (1969–1970)	Hungary	M, P, T	A, W, Sp, Su
50	Street (1975)	England	M	A, W, Sp, Su
51	Street (1977)	England	M	Sp, Su
52	Suarez & Urios (1999)	Spain	M, P, T	W
53	Tamisier (1971)	France	T	A, W
54	Thomas (1981) ^d	United Kingdom	M, P, T	A, W
55	Thomas (1982)	United Kingdom	M, P, T	A, W
56	Tiussa (1972)	Finland	M, T	A, Su
57	Tubbs & Tubbs (1983)	United Kingdom	T	Unknown
58	Veiga (1991)	Egypt	T	Unknown
59	Zuur, Suter & Krämer (1983)	Germany	M, P, T	W, Su

^aStudy including duckling data.^bOnly seed data of teal diet.^cOnly invertebrate data of teal diet.^dOnly seed species not quoted in Thomas (1982).

M, mallard; P, pintail; T, teal; A, autumn; W, winter; Sp, spring; Su, summer.

difference of mean ranks between groups (r_B) and within groups (r_W):

$$R = (r_B - r_W) / [N(N-1)/4]$$

The output statistic provides R -values ranging from -1 to 1 , and a P -value to help in decision making: two sampled units are considered as similar when $R = 0$ and as totally different when $R = 1$ (or -1 , although negative values pose difficulties in interpretation, see Chapman & Underwood, 1999). The statistical significance of the observed R is assessed by permuting (1000 times) the grouping vector to obtain the empirical distribution of R under a null model. We based the ANOSIM for seeds on family grouping rather than species to limit the number of variables because the statistical unit here was study (and some studies provided data to family rather than to species level).

We then used generalized linear mixed models to test for the effect of species (mallard, pintail or teal), season (autumn: August to October; winter: November to January; spring: February to April; or summer: May to July) and their potential interaction (species*season) on seed mass, length and width. This latter analysis was performed to seed species level and each study was set as a random factor to structure the model and to take potential pseudoreplication into account (Pinheiro & Bates, 2000). Competing models were ranked using Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002) and plausible models were considered to be those within two AICc units of the best-approximating model (i.e. with the lowest AICc value).

Analyses were performed using *vegan*, *nlme* and *AICcmodavg* packages in R 2.11 (R development Core Team, 2010).

Results

The between-seasons ANOSIM revealed no differences (all $R < 0.025$; all $P > 0.19$). The ANOSIM, however, revealed a difference in diet composition between mallard and teal ($R = 0.05$, $P = 0.02$), but not between pintail and mallard, nor between pintail and teal ($R = 0.04$; $P = 0.11$ and $R = 0.005$; $P = 0.32$, respectively).

A significant effect of duck species was found for two of the three seed parameters (Table 2): seeds consumed by mallards had a significantly greater mass than those consumed by teal ($t = 2.32$; $P = 0.02$). The same trend was observed for mallard versus pintail, although this was not statistically significant ($t = 1.87$; $P = 0.06$). A similar pattern was found for seed length (mallard vs. teal: $t = 2.07$; $P = 0.04$; and mallard vs. pintail: $t = 2.06$; $P = 0.04$). Patterns for seed width were less clear-cut; the null model was the most parsimonious model (lower AICc in Table 2) and differences between mallard and teal, and mallard and pintail were non-significant ($t = 1.76$; $P = 0.08$ and $t = 1.11$; $P = 0.27$, respectively). Differences between teal and pintail were non-significant throughout (all $t < 0.41$; all $P > 0.68$). Overall, teal tended to use smaller seeds than pintail, and pintail tended

Table 2 Model selection output from generalized linear mixed models on seed mass ($N = 1668$, $N_{\text{studies}} = 39$), seed length ($N = 2151$, $N_{\text{studies}} = 41$) and seed width ($N = 2151$, $N_{\text{studies}} = 41$) covariates

	k	AICc	Δ AICc	ω_i	LL
Seed mass					
Duck	5	4624.6	0.0	0.79	-2307.3
Null model	3	4627.4	2.7	0.20	-2310.7
Season	6	4633.2	8.6	0.01	-2310.6
Duck \times season	14	4642.2	17.5	0.00	-2307.0
Seed length					
Duck	5	1921.5	0.0	0.75	-955.7
Null model	3	1923.9	2.3	0.23	-958.9
Season	6	1929.3	7.7	0.02	-958.6
Duck \times season	14	1936.9	15.4	0.00	-958.4
Seed width					
Null model	3	1323.5	0.0	0.56	-658.8
Duck	5	1324.2	0.6	0.41	-657.1
Season	6	1329.4	5.8	0.03	-658.7
Duck \times season	14	1340.9	17.4	0.00	-656.4

Duck species and season were used as explanatory. Variables, number of k, AICc, Δ AICc, Akaike weights ω_i and LL are provided.

k, estimated parameters; AICc, Akaike's information criterion corrected for small sample size; LL, likelihood.

to use smaller seeds than mallards (Fig. 1), although the three species all used a wide spectrum of seed sizes, ranging from 0.008 to 250.59 mg.

Discussion

Contrasting the largest (mallard) and the smallest (teal) species in the European dabbling duck guild, we observed significant differences in mean mass and size (especially length) of ingested seeds at the Western Palearctic flyway scale. On average, mallard consumed heavier, longer and wider seeds than teal, while pintail was intermediate with values that did not differ significantly from those of the two other duck species. Seed size was thus positively related to species-specific spacing of bill lamellae, which agrees with our predictions and previous studies (e.g. Nudds & Bowlby, 1984; Nudds & Wickett, 1994).

Nudds & Bowlby (1984) studied predator-prey size relationships in North American dabbling ducks by reviewing American diet studies. They suggested that interspecific variation in interlamellar spacing alone could lead to partitioning of prey by size; that is, ducks with lower lamellar density (i.e. wider interlamellar spacing) relying on larger prey. Such interspecific differences have been documented in some European studies of dabbling ducks (Nummi, 1993; Guillemain *et al.*, 2002), while others did not find any food partitioning among closely related duck species (Thomas, 1982; Nummi & Väänänen, 2001). Thomas (1982) compared the distance between maxillar lamellae and the frequencies of occurrence of certain foods of critical sizes (six seed species ranging from 0.5 to 5.5 mm and four animal taxa ranging from 0.3 to 1 mm) in the gut contents of four dabbling ducks (mallard, pintail,

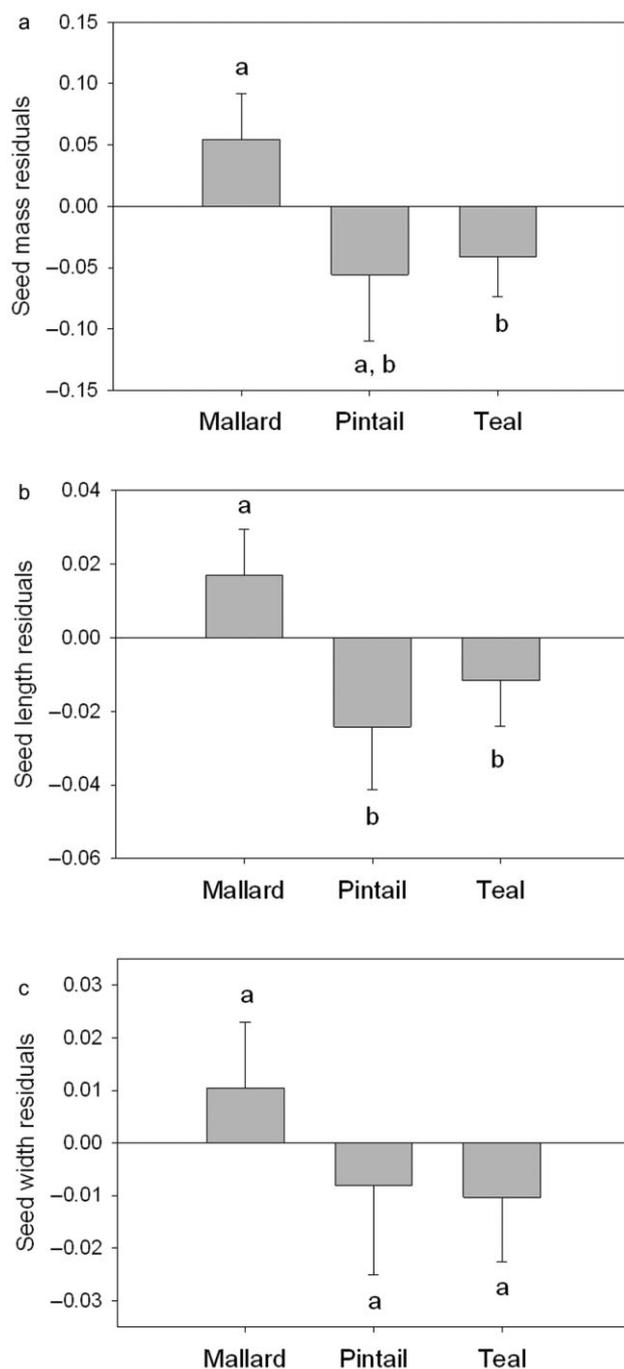


Figure 1 (a) Mass; (b) length; and (c) width residuals of ingested seeds by duck species, from the generalized linear mixed models null models. Error bars are standard error. The letters 'a' and 'b' refer to statistically significant differences.

teal and shoveler *A. clypeata*), and did not observe food partitioning by size, although small sample size and the limited size range considered may explain this. Nummi & Väänänen (2001) studied diet overlap among six sympatric dabbling

ducks (mallard, pintail, teal, shoveler, wigeon *A. penelope* and garganey *A. querquedula*) and failed to demonstrate any difference in diet size, proposing that the high level of diet overlap was promoted by abundant food resources in their study area (hence no competition). The latter studies are, however, typical snapshot studies. For the present meta-analysis, we used a very large compilation of data, from all over the flyway, and we were able to show that there are consistent differences in mean size of ingested seeds between species over large geographic areas and over seasons. The differences in seed diet therefore appear to have an important role in community structure, as lamellar density largely dictates which particle sizes are going to dominate the diet of individual ducks of a given species (see Gurd 2006 for details about the complexity of food filtering in dabbling ducks). Moreover, the ANOSIM analyses revealed that the seeds consumed by mallard and teal differ by family (and *a fortiori* species). The size segregation hence also reflects differences in seed species composition in the diet, which may also partly explain the coexistence of these two species under a paradigm of resource-limited competition-structured communities. Pintail, however presented similarities with mallard and teal diet. As stated earlier, the analyses are based on seed families. Segregation might also occur in a more subtle manner at the seed species level. Specializing in different food sizes (and species) may be an adaptation reducing niche overlap in times of high interspecific competition.

Apart from lamellar density, there are other physiological and ecological differences between species that may influence diet. Species with fewer lamellae (but larger, longer bodies) indeed tend to feed in deeper, open microhabitats, while species with denser lamellae (but smaller, shorter bodies) tend to feed in shallower and more vegetated microhabitats (Pöysä *et al.*, 1996; Pöysä & Sorjonen, 2000), which could also have an effect on food particle size through different plant composition. A combination of differences in bill lamellar density, body length and feeding habits may therefore be required for genuine food resource partitioning among dabbling ducks (cf. Nudds *et al.*, 2000; Guillemain *et al.*, 2002).

Despite a clear trend, we did not find unequivocal evidence for food segregation among all three duck species studied (pintail's diet overlap the ones of mallard and teal). Coexisting guild members with ecomorphological differences may, however, not always have clearly separated niches, but are likely to have similar preferences and exploit the same resources, at least opportunistically or during certain parts of the year if resources are not limited (Nummi, 1993; Guillemain *et al.*, 2002). In migratory species exploiting seasonally changing environments, resource limitation may occur only during some periods of the annual cycle, or even in some years only. Accordingly, on an annual basis, different species may show a high overlap in food resource use during some seasons. However, we did not find a significant effect of season. If competition does indeed increase during winter, when ducks tend to aggregate, a greater reduction in food overlap would have been expected (see Guillemain *et al.*, 2002).

We argue that the observed differences in average seed size in the diet of the three studied species are a result of different

lamellar density. The patterns of food size separation between the three species are compatible with the idea of coexistence under interspecific competition, a process that has long created harsh debate (e.g. Roughgarden, 1983). Our study thus supports the idea that interspecific competition may indeed be a structuring force in dabbling duck communities in the Western Palearctic, even if only intermittently so.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of all plant taxa found in the 59 duck diet studies (bf: bud/flower; sf: seeds/fruits; t: tuber; vg: vegetative part). Flora Europaea (Royal Botanic Garden Edinburgh, 2011) was used to name and group plant taxa.

Table S2. List of all animal taxa found in the 59 duck diet studies. Animal Diversity Web (University of Michigan Museum of Zoology, 2011) was used to name and group animal taxa.

Table S3. Mean mass (Arzel *et al.*, 2007; Brochet *et al.* unpub. data; Legagneux *et al.* unpub. data), length and width (Cappers *et al.*, 2006) of seed species used in the GLMM analyses. Flora Europaea (Royal Botanic Garden Edinburgh, 2011) was used to name and group plant taxa.

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