

# A flyway perspective on food resource abundance in a long-distance migrant, the Eurasian teal (*Anas crecca*)

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**Abstract** Two frequent assumptions about the evolution of long-distance migration in birds are that they travel long distances annually to reach food-rich areas for breeding, and that they time their migratory journey to be at staging sites when the latter provide the best feeding conditions. These assumptions have rarely been properly tested, and there is no study in which a species' major food types have been measured by standardized methods throughout a flyway and over a large part of the year. We here present such data for Eurasian teal (*Anas crecca*), converted to a common energetic currency, and collected at wintering, spring staging and breeding sites. Teal did not time migration to maximize local food abundance; most birds left wintering and spring staging sites before a sharp

increase in invertebrate food abundance occurred. On the other hand, hatching of ducklings coincided with a peak in invertebrate food abundance on boreal breeding lakes. Mean overall food abundance (invertebrates and seeds combined) did not differ between wintering sites in southern France and breeding sites in northern Sweden at the time of breeding. Our results are inconsistent with the hypothesis that long-distance migration in dabbling ducks has evolved because adult birds gain an immediate pay-off in increased food abundance by flying north in spring. However, our data confirm a selective advantage for breeding at higher latitudes, because hatching of ducklings may coincide with a peak in invertebrate emergence and because longer days may increase the duration of efficient foraging.

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## Introduction

A look in ecology textbooks or a search in the scientific literature databases show that food abundance is one of the first things ornithologists measure in order to understand their study species, be it its individual behaviour, its timing of reproduction or its population dynamics (Goss-Custard 1985; Daan et al. 1986; Newton 1998). Food abundance is one of the first factors considered when ornithologists attempt to understand patterns of individual behaviour, timing of reproduction or population dynamics of their study species (Berthold et al. 2003). Timing of breeding and migration in birds is often assumed to have evolved to match variations in food abundance (or availability) over the year. For example, the evolution of annual long-distance migration is frequently explained in terms of exploiting abundant

or more predictable food resources at higher latitudes in order to increase breeding success (Alerstam and Enckell 1979; Berthold et al. 2003). Another common assumption is that migration per se is timed to local peaks of food abundance at successive stopover sites in order to fuel the travel and to prepare for reproduction (Drent et al. 1978).

These and related hypotheses can be properly tested only if food resources are measured throughout the year and in all biomes where birds of a certain species or population occur. In a few migratory species food abundance has indeed been studied at sites geographically far apart within a flyway, notably swans, geese and shorebirds (e.g. Ens et al. 1990; Piersma et al. 1994; Beekman et al. 2002). To our knowledge, however, there is no study in which food resources of a migratory species have been (1) measured with consistent methods throughout a flyway, and (2) compared within the flyway by sampling wintering and staging areas also after the birds have left them. This is unfortunate, given the putative importance of food and resource competition to individual behaviour, population dynamics, and the dynamic nature of avian migratory patterns (Newton 1998; Krebs 2001; Alerstam et al. 2003).

According to theory, “capital breeders” prepare for reproduction by storing energy well ahead of breeding (often before or during migration in migratory species), whereas “income breeders” rely on food obtained on breeding grounds to survive and to produce eggs (Drent and Daan 1980; Bonnet et al. 1998). Given their relatively low body mass, dabbling ducks should theoretically all be income breeders (Meijer and Drent 1999; Klaassen 2002), especially so the smaller species like the Eurasian teal (*Anas crecca* L.; hereafter ‘teal’) (Paquette and Ankney 1998). This implies that teal rely largely on food at staging sites to fuel their spring migration and on food on the breeding grounds to breed successfully (Ankney et al. 1991; Alisauskas and Ankney 1992). However, published data do not allow for a comparison of food abundance among wintering, staging, and breeding areas for teal or other migratory dabbling ducks (*Anas spp.*). Moreover, studies of springtime food resource abundance in medium- and long-distance migrants are rare in their own right.

Adult dabbling ducks eat plant as well as animal matter, the conventional wisdom for most temperate zone species being that seeds and other plant material dominate the diet in fall and winter, and that invertebrates make up most of it in spring and summer (Cramp and Simmons 1977; Krapu and Reinecke 1992). It is important to income breeders to restore fat and protein reserves efficiently after spring migration, as egg formation and incubation are costly processes (Gatti 1983; Alisauskas and Ankney 1992). Accordingly, food abundance can influence wetland choice by breeding dabbling ducks during pair settlement and during brood-rearing (Pöysä et al. 2000). The importance

of invertebrate abundance to duckling survival during their first weeks of life is fundamental and well documented (Sugden 1973; Street 1977, 1978), a circumstance potentially affecting local population density as well as breeding success (Murkin and Kadlec 1986). For all these reasons, macroinvertebrate abundance, or factors affecting it, is often addressed when studying habitat choice, breeding success, and annual cycles in dabbling ducks (Batt et al. 1992). Previous diet studies nevertheless also indicate that the relative importance of aquatic plant matter such as seeds remains under-estimated in spring-staging and breeding dabbling ducks (e.g. Hesselman 1897; Green et al. 2002).

Eurasian teal/green-winged teal (*Anas crecca/A. carolinensis*) (Sangster et al. 2001) is one of the most abundant dabbling ducks globally (Delany and Scott 2006). Many aspects of their ecology are well studied, but summer and winter conditions have usually been considered separate from each other (reviews in Glutz von Blotzheim 1990; Batt et al. 1992). At first glance, previous research seems to verify that teal conform to the alleged general dabbling duck pattern of granivory in fall—winter and invertebrate-feeding in spring—summer (e.g. Cramp and Simmons 1977; DeRoia and Bookhout 1989; Glutz von Blotzheim 1990; Tamisier and Dehorter 1999). However, seeds from aquatic plants are common in the diet of breeding teal (e.g. Danell and Sjöberg 1980; DuBoway 1988; Nummi 1993, Table 1), and what spring-migrating individuals eat remains poorly documented. One reason is that few samples have been available historically due to the hunting season being closed at this time of year. Another is that the few published studies are based on gizzard contents only, rather than on oesophagus-gizzard samples (e.g. Coulter 1955); hence there is a lack of comparability because soft-bodied invertebrates are quickly digested and underrepresented in gizzard samples, compared to seeds. Teal reach many boreal breeding areas at a time of year when most nesting lakes are still ice-covered and the annual production of invertebrates has not yet started. There is no published information about food abundance in habitats utilized these final and potentially crucial spring weeks before egg-laying, but seeds from the previous year can be an abundant food resource in boreal habitats such as along flooded river banks (Nilsson and Grelsson 1990). Teal is the second earliest breeder among the dabbling ducks in Northern Europe, and there is a documented intraspecific fitness advantage of breeding early (Elmberg et al. 2005). Hence, there are proximate as well as evolutionary cost-benefit trade-offs in nesting early.

Our objective was to describe temporal and spatial abundance patterns of the major food types used by teal throughout its flyway in Western Europe. This was done by standardized sampling of invertebrates and seeds at sites, in

**Table 1** Importance of invertebrates and seeds in the diet of adult Teal *Anas crecca* wintering in France and breeding in Sweden

Country	Location	Seeds, plant material (%)	Invertebrates (%)	N	Month	Reference
France	Camargue	95.0	5.0	313	August–February	Tamisier and Dehorter 1999
	Brenne	96.9	3.1	88	September–January	Legagneux et al. unpub. data
	Normandy	94.1	5.9	147	September–January	Legagneux et al. unpub. data
	Western France	91.2	8.8	79	September–January	Guillemain and Fritz 2002
Sweden	Northern Sweden	13	85	7	August	Danell and Sjöberg 1980

Percentages were based on the abundance (number) of each alimentary item, except for Guillemain and Fritz (expressed as percent of dry mass)

microhabitats, and in patches where teal were actually foraging. Specifically, we studied: (1) the abundance of food resources in terms of seeds and invertebrates available at wintering, spring-staging, breeding, and moulting sites, (2) whether food resources in summer are more abundant at high latitudes than in wintering and staging areas that the birds have left. This is a key assumption of the hypothesis that food abundance is a driving force behind the evolution of long-distance migration in birds (Batt et al. 1992; Berthold et al. 2003).

## Methods

### Migratory pattern and study sites

Many of the teal wintering in France migrate through Western Europe on their way to and from breeding grounds in Scandinavia and Finland (Scott and Rose 1996; Fransson and Pettersson 2001; Wernham et al. 2002; Bakken et al. 2003; Guillemain et al. 2005). The monthly mean position (latitude–longitude) of adult as well as first winter teal ringed in Sweden is located in France throughout the winter (December–February) (Fransson and Pettersson 2001). For the present study we selected four sampling regions within the rather well defined flyway of this Fennoscandian breeding population (cf. Koskimies 1956; Solonen 1985; Fransson and Pettersson 2001; Scott and Rose 1996).

The Camargue, which is the most important wintering area for dabbling ducks in France, was used as a reference wintering ground (Fig. 1). Normandy in Northern France was used as the first of two spring staging areas, and wetlands in Scania in southern Sweden as the second. Lakes in Västerbotten, north-central Sweden, represented moulting and breeding sites. From March 2003 to August 2004 we sampled invertebrate prey in 13 wetlands and lakes in these regions, while seeds were sampled in 10 of them, starting in May 2003 (Fig. 1, Table 2). All study sites were selected because of their documented local or regional importance for teal.

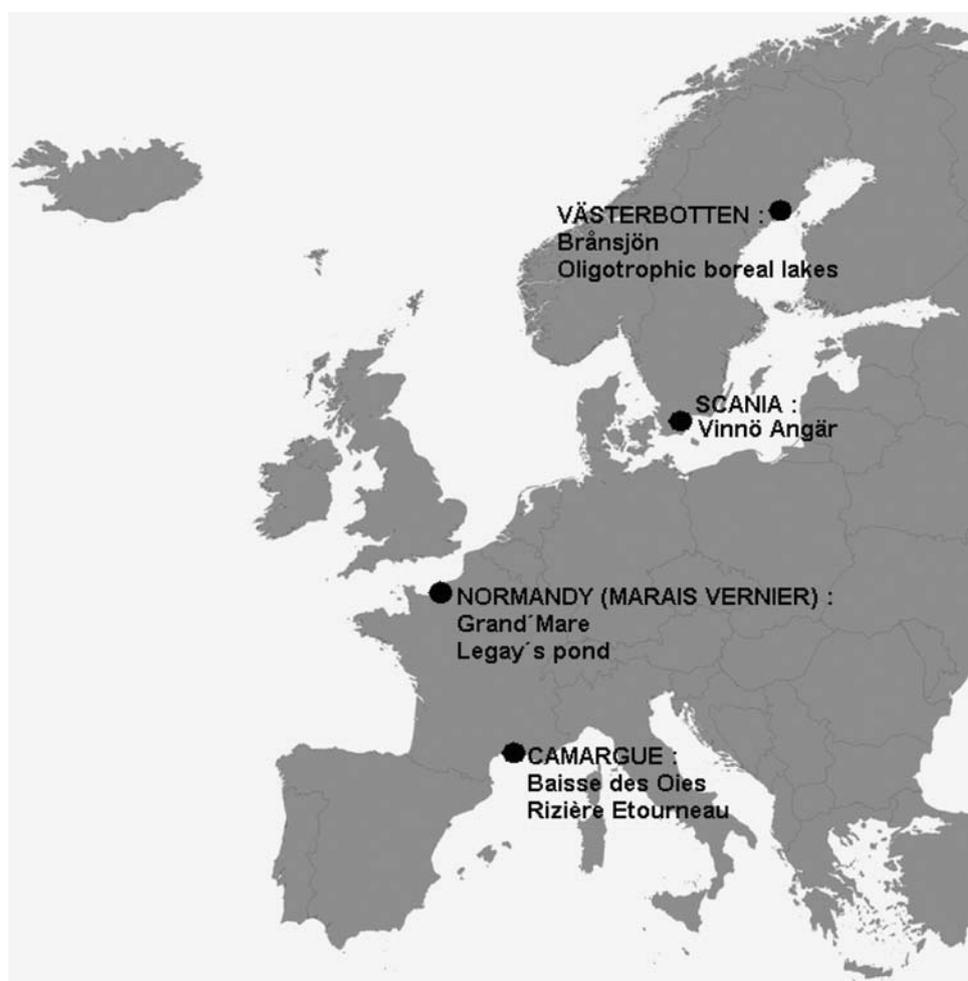
In the Camargue, we used the wetlands of Les Marais du Vigueirat, which host approximately 15,000 wintering teal (Tamisier and Dehorter 1999). In winter as well as in the early part of spring migration, dabbling ducks generally rest during the day and depart at dusk to access nearby nocturnal foraging sites (Tamisier and Dehorter 1999). Thus, we measured food abundance at a day roost and a nocturnal foraging site (Table 2), both of which are typical shallow Mediterranean wetlands that dry up in late summer (see below). We collected invertebrate data weekly at both sites, while seed samples were obtained from the nocturnal foraging habitat only.

In the southern spring-staging area, in Normandy, we selected two sites in the Marais Vernier area. The nature reserve of the Grand'Mare is one of the most important day roosts in the region (Clairefond and Schricke 1994). Here, too, most of the ducks leave at dusk for nearby nocturnal foraging sites. To represent the latter we sampled the Legay's pond, located only 1,400 m from the Grand'Mare day roost. The fact that the Grand'Mare is the major day roost of the area further supports the assumption that the same birds used both sites. Food samples were collected once a week at both sites.

Southern Scandinavia is a little more than half-way along the migratory journey for teal breeding in boreal Western Europe. We took weekly samples at the alluvial pasture Vinnö Ängar in the province of Scania, Sweden. The site is part of the biosphere reserve 'Kristianstads Vattenrike', a complex of wetlands and seasonally flooded meadows. In contrast to the Grand'Mare, Vinnö Ängar was utilized by teal both as a diurnal foraging site and as a night roost.

We used seven lakes in the Umeå area in the province of Västerbotten, north-central Sweden, of which six were typical boreal teal breeding lakes; i.e. small, oligotrophic, surrounded by coniferous boreal forest, and with shores dominated by floating peat bog (chiefly *Sphagnum spp.*). The seventh lake, Brånsjön, is much larger, eutrophic, surrounded by cereals and hayfields. It is used by thousands of dabbling ducks as a staging site in spring, and by hundreds for breeding and moulting. Brånsjön was sampled

**Fig. 1** Study areas within the flyway of teal *Anas crecca* in Western Europe



**Table 2** Study sites and sampling periods for invertebrates and seeds

Sampling site	Status	Sampling period	Number of invertebrate samples	Number of seed samples	
Camargue (Marais du Vigueirat 43°31'N, 04°46'E)	Baisse des Oies	Day roost	29/10/2003 to 21/07/2004 <sup>a</sup>	195	–
	Rizière Etourneau	Foraging site	28/10/2003 to 25/05/2004 <sup>b</sup>	155	95
Normandy (Marais Vernier 49°25'N, 0°32'E)	Grand'Mare	Day roost	01/03/2003 to 18/03/03 and 21/02/2004 to 24/03/2004	82	52
	Legay's Pond	Foraging site	26/02/2004 to 10/03/2004	28	36
Scania 56°02'N, 14°05'E	Vinnö Ängar	Resting and foraging site	06/04/2004 to 25/04/2004	40	60
Västerbotten 64°N, 20°E	Brånsjön	Resting and foraging site	14/05/2003 to 30/07/2003 and 18/06/2004 to 27/07/2004	220	370
	Six oligotrophic breeding lakes	Resting and foraging sites	27/05/2003 to 31/07/2003 and 18/06/2004 to 27/07/2004	189	612

<sup>a</sup> Seeds were not sampled at Baisse des Oies

<sup>b</sup> At Rizière Etourneau, seeds were only sampled from 06/01/2004 to 11/05/2004

<sup>c</sup> In Normandy, seeds were only sampled in 2004

weekly, whereas the oligotrophic lakes were sampled every second week.

We thus sampled temporary wetlands, coastal meadows, coastal lagoons, fluvial meadows, as well as lakes of different trophic status. On each study day, and as part of a more extensive research program, foraging behaviour of dabbling ducks was studied before the sampling of food resources (Arzel et al. 2007; Guillemain et al. 2007). Invertebrate and seed samples were taken in macro- and microhabitats where teal and other dabbling ducks were actually seen foraging and/or where faeces, footprints and feathers indicated recent foraging activity. In this way we strived to ensure that samples truly represented the food items normally encountered by foraging teal. The precise locations where the samples were collected were randomized within each foraging habitat. The sampling methods were strictly standardized among sites, being described below.

### Invertebrate sampling

Aquatic invertebrates were caught using one-litre activity traps (Murkin et al. 1983, procedures described in Elmberg et al. 1993) placed horizontally along the shore at depths ranging from 5 to 30 cm in order to cover the feeding range of dabbling ducks. In the Camargue we used five traps at each site on each sampling occasion. In Normandy, Scania, and Västerbotten ten traps were used. Activity traps catch epibenthic as well as nektonic animals. They assess the abundance of invertebrate prey currently available to ducks where the latter actually forage, which is not necessarily (and does not aim at being) a measure of the overall productivity of a wetland.

Activity traps were in operation for 24 h. At emptying the contents were passed through a 1 mm mesh sieve, but all visible smaller invertebrates that passed through it were also collected and identified, for example *Ostracoda*, *Copepoda*, *Cladocera*, *Nematoda* and larvae of *Heteroptera*. This corresponded roughly to a minimum prey size of 0.3 mm. Note that, traps which contained fish and newts were systematically excluded to avoid biases as they could affect reliability of catches (Elmberg et al. 1992). Invertebrates were counted and identified to order or family. The catch from each trap was analysed separately. Although meiofauna may occur in the diet of teal (e.g. Gaston 1992), the minimum size of food items that ducks catch effectively is largely determined by the space between the bill lamellae, being as small as 0.3 mm in Northern Shoveler (*Anas clypeata*) and 1 mm in Mallards (*Anas platyrhynchos*) (Nudds and Bowlby 1984, Tolkamp 1993). The other European dabbling ducks, teal included, fall between these values. Adult teal mainly eat food items smaller than 12.5 mm (Tamisier and Dehorter 1999), i.e. within the size

range of all important prey types encountered in this study. Larger prey is relatively rare in most lakes and some of the former are probably difficult to handle for a small duck. During their first two weeks of life *Anas* ducklings feed largely on *Chironomidae* (Street 1977; Bengtson 1975; Krapu and Swanson 1978; Danell and Sjöberg 1977), most of which fall into the 7.6–12.5 mm length category (Nudds and Bowlby 1984). For the present study we accordingly used data for all invertebrates ranging from 0.3 to 12.5 mm (Tolkamp 1993; Mott 1994; Gaston 1992).

Using the calorific densities in Table 2 in Nudds and Bowlby (1984) and literature data on invertebrate mass (Driver et al. 1974; Dumont et al. 1975; Meyer 1989; Stead et al. 2003), we converted our catches to express their content of available energy (KJ/cm<sup>3</sup>) by site, date, and prey size category. Note that this concerns food energetics, and not prey preferences that ducks may have. As there was no available information about the calorific density of *Plecoptera*, we used the same value as for *Ephemeroptera*, a very similar type of insect. *Planaria* were excluded from the analyses because there is no indication in the literature that dabbling ducks eat them.

### Seed sampling

We used a cylindrical corer (10 cm tall, 7.2 cm in diameter); to obtain 5–18 samples of strictly the same sample volume (407 cm<sup>3</sup>), in each wetland on each sampling date; i.e. 4–6 per shoreline microhabitat. Core samples comprised the upper 10 cm of vegetation and barer sediments in the case of a gently sloping shoreline, including any floating seeds intercepted as the corer was submerged. The latter was true for shoreline microhabitats made up of floating vegetation too, but here cores did not reach down to inorganic substrates. In all cases the upper level of the sample core was at a depth well within reach of up-ending teal, i.e. cores assessed the abundance of seeds actually available to foraging ducks, not necessarily the full seed-bank. Each core was emptied in a plastic bag for later sorting and identification in the laboratory, where it was passed through several sieves, the smallest having a 0.3 mm mesh size for the same reason as for the invertebrate samples. All seeds were then sorted under a binocular microscope, oven-dried at 60°C until desiccation, i.e. for at least 24 h, and later identified by the same observer (F. B.) using Beijerinck (1947); Berggren (1969, 1981) Anderberg (1994) and a few internet sources (<http://www.bioimages.org.uk/> and [http://www.dijon.inra.fr/malherbo/hyppa/hyppa-f/hyppa\\_f.htm](http://www.dijon.inra.fr/malherbo/hyppa/hyppa-f/hyppa_f.htm)).

We weighed as many seeds as possible of each of the 66 taxa encountered (54 identified to species and 12 to genus). Rice (*Oryza sativa*) was the only species for which we used a seed weight value from the literature (Tamisier 1971a). In

a few species ( $N = 7$ ) for which seed mass was not available we used the mean weight for the genus as a whole. For three genera we either had too few seeds to get precise data per species or no species-level data at all, in which cases we used the mean weight for the genus as a whole. Finally, in the family *Asteracea* we used the mean weight of all seeds for those that were not identifiable to species or genus.

To convert seed mass to available energy we used calorific density data in Sugden (1973); Paulus (1982); Hoffman and Bookhout (1985), and Joyner et al. (1987), but also some complementary measurements of the most abundant seeds in our own sample. For this we (P. L.) weighed seeds to the nearest 0.001 g and freeze-dried them to constant mass in liquid nitrogen. The energy content was determined on dry aliquots (0.3–1 g) using an adiabatic bomb calorimeter Parr 1241 with benzoic acid as standard (Parr Instrument Co., Moline, Illinois, USA). Species-specific calorific density data were available only for seven of the species in our sample. For species and genera lacking energy value data, we either averaged available data per genus ( $N = 12$  species and 5 genera) as above for seed mass, or when genus level data were not available either, per family after checking that seed weights were fairly homogenous within each group, respectively (e.g. *Alismataceae*: min =  $1.6 \text{ E-}4$ , max =  $3.1 \text{ E-}4$ , mean  $\pm$  SE =  $2.4 \text{ E-}4 \pm 0.2 \text{ E-}4$ ; *Asteracea*: min =  $0.1 \text{ E-}4$ , max =  $26.4 \text{ E-}4$ , mean  $\pm$  SE =  $12 \text{ E-}4 \pm 2.5 \text{ E-}4$ ; *Chenopodiaceae*: min =  $0.6 \text{ E-}4$ , max =  $21.6 \text{ E-}4$ , mean  $\pm$  SE =  $5.7 \text{ E-}4 \pm 1.3 \text{ E-}4$ ; *Poaceae*: min =  $0.6 \text{ E-}4$ , max = 0.25, mean  $\pm$  SE =  $0.02 \pm 0.01$ ; *Cyperaceae*: min =  $0.4 \text{ E-}4$ , max =  $36.5 \text{ E-}4$ , mean  $\pm$  SE =  $9.9 \text{ E-}4 \pm 1.2 \text{ E-}4$ ;  $N = 16$  species, seven genera and the *Asteracea* family). Finally, when genus or family level data were not available, or when weights differed considerably within a family ( $N = 19$  species and 10 genera), we used the mean calorific density of seeds with similar weight; energy content was similar across the families tested (mean 20,068 KJ/g  $\pm$  0.222 SE). Seeds as well as invertebrates may differ in terms of digestibility. The “ideal” measurement would thus be the ‘true metabolizable energy’ (Ballard et al. 2004). However, such digestibility data, which is usually determined by feeding single food items, are not available for omnivores like teal.

### Statistical analyses

When compiling and analyzing data we divided the year into five periods: breeding (June–July), post-breeding and fall migration (August–September), wintering (October–January), early spring migration (February–March), and late spring migration (April–May). To avoid pseudo-replication we averaged caloric density by site and date

separately for core (seed) and invertebrate trap samples. We used these averages in the statistical analyses, but all data were log-transformed to fulfil requirements of normality (post-transformation test statistics: Kolmogorov–Smirnov  $d = 0.10$  and  $0.065$  for seeds and invertebrates, respectively, Lilliefors  $P$  non-significant in both cases). General Linear Models (Statistica 6.0, Statsoft Inc 2002) were used to test for differences in average calorific density between sampling sites and periods of the year. When appropriate, the Bonferroni post-hoc  $t$  test (threshold value for significance at 0.05) was applied to determine which sites differed from each other.

### Results

No between-year differences in food caloric density were detected at sites measured in more than 1 year [invertebrates: Grand’Mare ( $F_{(1,6)} = 0.409$ , NS); Brånsjön ( $F_{(1,20)} = 1.108$ , NS); Breeding lakes ( $F_{(1,5)} = 1.610$ , NS); Seeds: Brånsjön ( $F_{(1,22)} = 0.939$ , NS); breeding lakes ( $F_{(1,5)} = 1.777$ , NS)]. Likewise, no interaction occurred between site and year. Consequently, data from the 2 years were pooled at all sites.

#### Flyway patterns of invertebrate calorific density

Starting on the wintering grounds, the day roost (Baisse des Oies) had significantly higher invertebrate calorific density than the foraging site Rizière Etourneau (October–January; Table 3). Overall invertebrate calorific density peaked in March–April at both Camargue sites, when most ducks had already left the area.

In February–March (early spring migration), the staging areas in Normandy offered a significantly higher calorific density of invertebrates than the Camargue wintering areas which the ducks had just left (Table 3; Fig. 2a). This was especially evident for the nocturnal foraging site in Normandy.

In April–May (late spring migration) there was no significant difference between sites far apart in the flyway (i.e. the Camargue, Vinnö Ängar, and Brånsjön) in terms of invertebrate calorific density. However, the Camargue wintering sites still tended to offer higher calorific density of food than Vinnö Ängar. Finally, when all breeding lakes were sampled in late spring, the eutrophic Brånsjön had higher values than the nearby oligotrophic lakes (Table 3).

In June–July (breeding season), invertebrate calorific density was more than fourteen times higher at Brånsjön than at the oligotrophic breeding lakes (Table 3). A clear abundance peak was observed at Brånsjön around 22 June in 2003 and around 1 July in 2004 (Fig. 2a). Despite this, there was not any significant difference between Brånsjön

**Table 3** Mean calorific density (KJ/cm<sup>3</sup> ± SE) of invertebrates per sampling period

	Early spring migration	Late spring migration	Breeding	Fall migration	Wintering
Baisse des Oies	0.651 ± 0.125 (8)	1.983 ± 0.261 (9)	3.904 ± 0.674 (8)		0.661 ± 0.181 (14)
Rizière	0.398 ± 0.104 (8)	2.018 ± 0.383 (9)			0.189 ± 0.042 (14)
Etourneau					
Grand'Mare	1.513 ± 0.278 (8)				
Legay's Pond	2.514 ± 0.516 (3)				
Vinnö Ängar		0.827 ± 0.110 (4)			
Brånsjön		1.303 ± 0.268 (4)	8.136 ± 2.258 (16)	14.646 ± 0.451 (2)	
Oligotrophic breeding lakes			0.566 ± 0.166 (7)		
GLM	$F(3,23) = 11.151,$ $P = 0.0001$	$F(3,22) = 3.249,$ $P = 0.0413$	$F(2,28) = 19.850,$ $P = 0.000004$		$F(1,26) = 5.317,$ $P = 0.029$

Number of sampling days in brackets. GLM results are based on log-transformed data

and the Camargue winter day roost, Baisse des Oies, at this time of year (post-hoc Bonferroni tests; Table 3), a critical result with respect to the hypotheses addressed. However, the variance around means was rather large for both places, suggesting that Brånsjön nonetheless may be slightly more productive than the Camargue. All August samples were from Brånsjön, preventing any comparison between sites at this time of year.

Finally, a comparison between sampling periods, without consideration of site, revealed a consistent temporal trend within the flyway, i.e. invertebrate calorific density increased significantly from October to August ( $R^2 = 0.50$ ,  $F(4,112) = 28.42$ ,  $P < 0.000001$ ; Table 3, Figs. 2, 3). A similar increasing trend was observed for the variance around these means, indicating that invertebrate food resources became less predictable at the study sites as the season progressed.

#### Flyway patterns of seed calorific density

In February–March (early spring migration), Rizière Etourneau, the nocturnal foraging site in Camargue, had significantly higher seed calorific density than the Grand'Mare, the Normandy day-roost, while Legay's pond, the Normandy nocturnal foraging habitat, was intermediate (Table 4; Fig. 2b).

In April–May (late spring migration), seed calorific density was much higher at the winter foraging site than at any staging or breeding site (Table 4): the value for Rizière Etourneau was three times higher than that for Vinnö Ängar, and four times higher than that for the eutrophic boreal Brånsjön (Table 4).

In June–July (breeding season), the Camargue nocturnal foraging habitat had dried up completely, so that only data from Brånsjön and the six other breeding lakes were available. Seed calorific density did not differ significantly between Brånsjön and the oligotrophic lakes (Table 4).

A comparison of energy amounts available as seeds between sampling periods revealed a significant temporal flyway level pattern ( $R^2 = 0.322$ ,  $F(4,58) = 6.885$ ,  $P = 0.0001$ ). Bonferroni-adjusted *t* tests showed that seed calorific density was lower during the breeding season than during any part of the wintering and spring migration periods, and that the latter two did not differ from each other. Variance of seed calorific density showed a similar pattern, i.e. it was lower during the breeding season than at any other time along the migratory route.

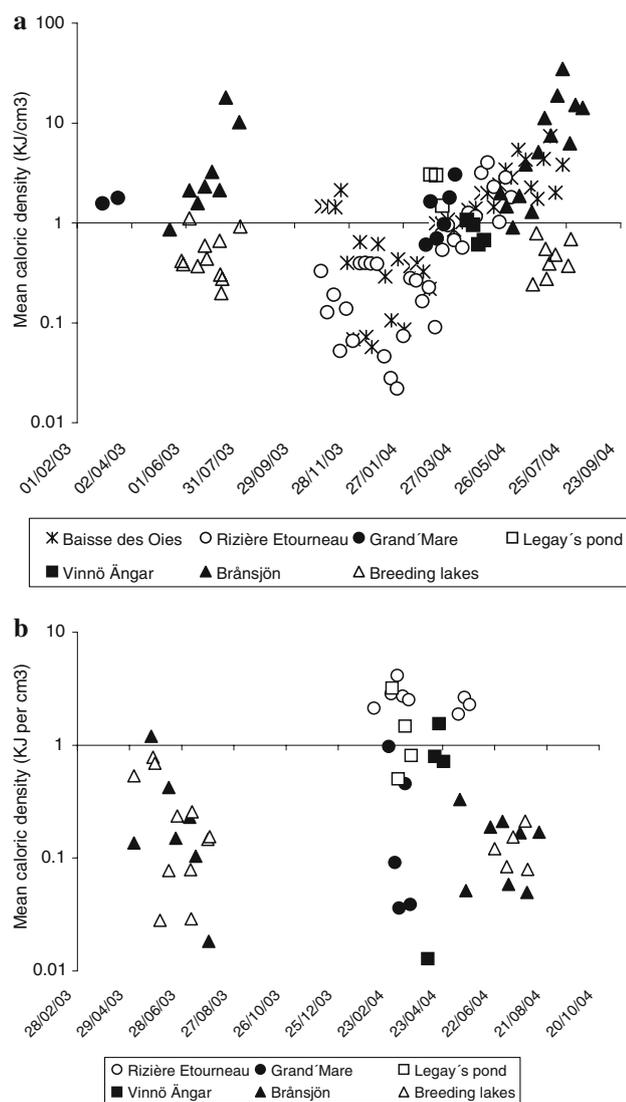
#### Combined patterns

When comparing the general trends of invertebrate and seed calorific densities within the flyway and from winter to summer, we observed that the former food category increased, whereas the latter decreased (Fig. 3). Invertebrate food energy was more abundant than energy available as seeds for most of the year, but the use of different sampling methods for the two food types may bias this interpretation (see below).

## Discussion

#### Flyway patterns of food abundance

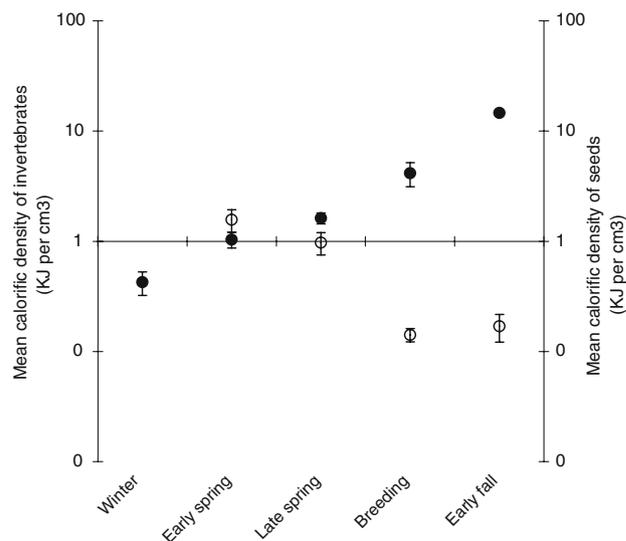
This is the first study of a long-distance migrating duck documenting the general levels and variation of the food types in its diet and expressing them in a common currency. That invertebrate food was relatively scarce in winter is consistent with earlier studies showing that teal are mainly granivorous at this time of the year (Tamisier 1971b). Although invertebrate calorific density differed significantly between the day-roost and the nocturnal foraging habitat in winter, both values were among the lowest recorded anytime of the year, when seed calorific density at



**Fig. 2** Mean  $\pm$  SE calorific density ( $\text{KJ}/\text{cm}^3$ ) of invertebrates (**a**) and seeds (**b**) per site (Log-scale)

the foraging site (no data being available at the day roost) was the highest. Teal have been reported to dramatically increase the proportion of invertebrates in the diet later in spring and summer (Tamisier 1971b, Pehrsson 1984). Indeed, such a change seems feasible and probably adaptive in our study system, given that there was a spatially consistent increase in mean calorific density of invertebrates in spring.

Mean invertebrate calorific density kept on increasing as teal moved north within the flyway, well into summer. At Brånsjön, a peak of invertebrate abundance was observed in late June–early July, coinciding with the hatching peak of ducklings in that study area (C. A., pers obs). At this time of year there were more invertebrate prey in Brånsjön than in the neighbouring oligotrophic breeding lakes, a pattern consistent with the far higher density of breeding



**Fig. 3** Mean  $\pm$  SE calorific density ( $\text{KJ}/\text{cm}^3$ ) of invertebrates (full circle, left axis) and seeds (empty circle, right axis) per sampling period. We used the mean calorific data from the sites where teal actually were; i.e. Camargue for the winter period, Normandy for early spring, Scania and Västerbotten for late spring and Västerbotten for breeding and early fall (Log-scale)

ducks at the former. Although variance was higher and predictability thus lower, mean calorific density of invertebrates at Brånsjön was not significantly different from what the ducks would have encountered at the Camargue sites at this time of year should they have stayed there.

Specifically, invertebrates may live off stored energy for a large part of the winter and consequently be less profitable in terms of metabolizable energy in spring than they are in summer or fall (Driver et al. 1974). Future work also needs to consider the possibility that prey utilization differs significantly from prey availability (Bartonek and Hickey 1969; Weller 1988). In addition, energy is probably not all that matters; Sugden (1973) stressed the significance of a mixed diet for ducklings in order to meet their nutritional needs, and Street (1978) demonstrated the importance of a mixed diet for weight gain.

Generally speaking, and before drying up in summer, the Camargue nocturnal habitat offered more seed food than any other site. This is again consistent with previous studies showing that teal are mainly granivorous in winter (Tamisier and Dehorter 1999). Seed abundance did not increase during summer, although late summer is when most aquatic plants release their seeds in both the Mediterranean (Mesléard, pers. comm.) and the boreal breeding areas. Obviously, our sampling ceased before the main seed fall.

We observed opposite annual temporal trends in invertebrate calorific density as compared to seeds (Fig. 3). It is noteworthy that the spring-time drop in seed food

**Table 4** Mean calorific density (KJ/cm<sup>3</sup> ± SE) of seeds per sampling period

	Early spring migration	Late spring migration	Breeding	Fall migration	Wintering
Rizière	2.713 ± 0.327 (6)	2.009 ± 0.372 (9)			2.112 ± 0.288 (4)
Etourneau					
Grand'Mare	0.319 ± 0.181 (5)				
Legay's Pond	1.501 ± 0.607 (4)				
Vinnö Ängar		0.768 ± 0.314 (4)			
Brånsjön		0.481 ± 0.278 (6)	0.198 ± 0.036 (16)	0.169 ± 0.118 (2)	
Oligotrophic breeding lakes		0.442 (1)	0.142 ± 0.021 (6)		
GLM	$F(2,12) = 12.957,$ $P = 0.001$	$F(3,16) = 3.423,$ $P = 0.043$	$F(1,20) = 0.004,$ $P = 0.950$		

Number of sampling days in brackets. GLM results are based on log-transformed data

coincided with a dramatic increase in invertebrate abundance, and that both occurred when teal are supposed to switch diet in favour of invertebrates (Tamisier 1971b; Pehrson 1979). We have previously demonstrated that foraging activity in teal increases during spring migration, especially so diurnally (Arzel et al. 2007). This is concomitant with an evident decrease in predator disturbance (Arzel et al. 2007; Guillemain et al. 2007) as well as an increase in foraging depth (Guillemain et al. 2007). Hence, reduced predation risk and longer days as teal move north permit them to increasingly rely on riskier underwater sight-feeding. In this way they can shift the foraging focus from seeds to moving invertebrates in the water column as they move north, a notion correlating well with the general abundance patterns of the two food types (cf. Fig. 3). Our study thus provides a general causative explanation for proximate as well as evolutionary patterns of food selection and diet shifts in long-distance migrating teal in Western Europe.

However, the relative importance of the two food types can still not be assessed conclusively: core samples assess what there is in the upper layer of the shore substrate, whereas activity traps catch mobile prey that accumulate in the container. On top of this difference between “active” and “passive” sampling, the actual profitabilities of the two food categories to ducks depend on foraging mode in combination with microhabitat structure. As gut samples were not collected, we cannot draw any firm conclusions about diet selection and whether it conforms to the abundance patterns observed.

Teal are known to aggregate in large flocks during the day in winter (Tamisier and Dehorter 1999). During the breeding season, however, they have access to an overabundance of boreal lakes, leading to low densities of birds per wetland and to many suitable sites remaining unused (Elmberg et al. 2005). In a related study, Arzel et al. (2007) found a positive relationship between teal foraging time and densities of both teal and other dabbling ducks. This is

consistent with the idea that food is not limiting; alternatively, it could indicate that teal offset costs of higher food competition for benefits of improved predator vigilance and dilution effects provided by larger flocks (Guillemain et al. 2002, 2007).

#### Evolutionary implications

Although there was a consistent annual temporal increase of invertebrate food abundance where the teal actually were (i.e. sampled as they migrated north), we did not find a higher mean abundance in late spring and summer on ‘normal oligotrophic boreal breeding lakes’ than on the wintering sites in Camargue at the same time. Seed abundance data yielded a similar result, and together these patterns could be interpreted as refuting the hypothesis that better feeding opportunities at high latitudes in summer explain the evolution of long-distance migration (cf. Batt et al. 1992; Berthold et al. 2003). In general terms, and for adult birds, this may be the case if average food abundance per se is considered. Our data indicate no obvious direct pay-off for flying even a little ways north, as the energy spent by doing so is not compensated for by more abundant food. Such a conclusion about a lack of selective advantage may change, though, if there is a consistent pattern of increased between-site variance in food abundance going north (Fig. 3), and if teal also manage to find and exploit the better sites.

Assuming that another process has driven the evolution of migration, local food abundance patterns may also be seen *ad hoc* as a timing issue; in other words, is each site utilized by teal during its annual peak of food abundance? Starting from the winter grounds this does not seem to be the case either. Invertebrate calorific density peaked in the Camargue in March–April, i.e. well after teal had departed (Guillemain et al. 2006). Similarly, Arzel and Elmberg (2004) observed transient dabbling ducks, including teal, to leave a spring staging site very close to Vinnö Ängar in

southern Sweden prior to a dramatic increase in invertebrate food abundance. Our results are consistent, however, with the idea that dabbling ducks time their migration and breeding so that ducklings hatch when invertebrate food is the most abundant on boreal lakes; a timing that may be crucial for survival during the first weeks (cf. Sugden 1973; Bengtson 1975; Street 1977; Danell and Sjöberg 1977, 1982; Sjöberg and Danell 1982; Pehrsson 1984; Hill et al. 1987; Robinson et al. 2003; Elmberg et al. 2005). Although our data do not explain the genesis of long-distance migration in teal, they do demonstrate a present selective advantage of a migratory pattern and timetable that optimise feeding conditions for ducklings rather than for migrating adults.

There are indeed further and competing hypotheses to explain the timing of long-distance migration in dabbling ducks. The present study was not designed to explicitly test these, but our results still provide some insights for future research. First, predation risk for adults as well as nests appears to be higher in wintering than in breeding areas (Guillemain et al. 2007, Elmberg et al. submitted). Secondly, the Camargue sites dried up in late summer, as most Mediterranean wetlands do. Nesting fidelity may be related to annual water levels, as shown for Northern Shoveler (Blums et al. 2002), suggesting that wetland predictability rather than crude food abundance may select for migration, site fidelity and female-biased philopatry to evolve (Alerstam and Enckell 1979; Rohwer and Anderson 1988; Anderson et al. 1992; Robertson and Cooke 1999; Doherty et al. 2002; Blums et al. 2002). Thirdly, interspecific competition for breeding sites has been hypothesized to account for the evolution of long-distance migration. Indeed, there is an almost unlimited number of lakes and wetlands in Fennoscandia and Russia on which ducks wintering in Western Europe can space out, but a large proportion of them do not have breeding teal anyway (Elmberg et al. 2005), and the prevalence of food limitation in these systems remains uncertain (see above, Elmberg et al. 2003; Gunnarsson et al. 2004). Female ducks exhibit a high breeding (Rohwer and Anderson, 1988; Anderson et al. 1992; Doherty et al. 2002; Blums et al. 2002) and wintering (Robertson and Cooke 1999) site fidelity. Such philopatry may be an evolutionarily stable strategy if the geographic areas—if not the habitats—used are sufficiently predictable when it comes to water level and food resources. Finally, a combination of food abundance per se and long days may explain long-distance migration in ducks. Even at moderate boreal latitudes, like those in the present study, there is continuous daylight from early May until early August. Such conditions may be advantageous for ducklings as well as for adults in the sense that sight-feeding is more efficient than touch-feeding, especially when mobile aquatic invertebrates are the preferred prey.

The present study thus lends some support to the second of these alternative hypotheses, but further documentation of food abundance, diet choice and food profitability at key sites within the flyway of European teal is needed in order to confirm these patterns and to formulate experimentally testable hypotheses.

## Zusammenfassung

Betrachtung der Nahrungsverfügbarkeit auf den Zugrouten eines Langstreckenziehers, der Krickente (*Anas crecca*)

Zwei häufige Hypothesen zur Evolution von Langstreckenzug bei Vögeln sind, dass sie jährlich weite Strecken zurücklegen um in nahrungsreiche Brutgebiete zu gelangen, und dass sie ihren Zug zeitlich regulieren um dann in Rastgebieten zu sein, wenn diese die besten Nahrungsbedingungen bieten. Diese beiden Hypothesen sind selten adäquat getestet worden, und es gibt keine Untersuchung, in der die wesentlichen Nahrungskomponenten einer Art entlang eines Zugwegs und über einen großen Zeitraum des Jahres standardisiert erfasst wurden. Hier stellen wir für die Krickente (*Anas crecca*) solche Nahrungsdaten vor, die wir in Winterquartieren, Rastgebieten auf dem Zug und in Brutgebieten erhoben und in eine gebräuchliche Energieeinheit umgerechnet haben. Die Krickente stimmte ihre Zugzeit nicht auf die jeweils maximal vor Ort verfügbare Nahrungsmenge ab; die meisten Vögel verließen ihre Überwinterungsgebiete und Frühjahrsrastgebiete bereits bevor es zu einem steilen Anstieg der verfügbaren Nahrungsmenge in Form von Evertebraten kam. In den borealen Seen im Brutgebiet fiel der Schlupf der Entenküken jedoch zeitlich mit einem Höchstwert an verfügbarer Evertebratennahrung zusammen. Die gesamt gemittelte Nahrungsmenge (Evertebraten und Samen zusammengenommen) unterschied sich nicht zwischen Winterquartieren in Südfrankreich und Brutgebieten in Nordschweden zur Brutzeit. Die Hypothese, dass sich Langstreckenzug bei Schwimmenten entwickelt hat, weil Altvögel einen unmittelbaren Vorteil in Form eines erhöhten Nahrungsangebots haben, wenn sie im Frühjahr nach Norden fliegen, steht im Widerspruch zu unseren Ergebnissen. Dennoch bestätigen unsere Daten einen Selektionsvorteil für eine Reproduktion in höheren Breiten, weil der Schlupf der Küken dort womöglich zeitlich mit einem Höchstwert im Auftreten von Evertebraten zusammenfällt und weil größere Tageslängen die Dauer effizienter Nahrungssuche erhöhen könnten.

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