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Time use, foraging behavior and microhabitat use in a temporary guild of spring-staging dabbling ducks (*Anas spp.*)

Céline Arzel & Johan Elmberg*

Arzel, C., (a) Department of Mathematics and Natural Sciences, University of Kristianstad, SE-291 88 Kristianstad, Sweden, (b) Office National de la Chasse et de la Faune Sauvage, Le Sambuc, F-13200 Arles, France, (c) Laboratoire d'Ecologie des Hydrosystèmes, Université Paul Sabatier, 118 route de Narbonne, F-31062 Toulouse, France
*Elmberg, J., Department of Mathematics and Natural Sciences, University of Kristianstad, SE-291 88 Kristianstad, Sweden (*Corresponding author's e-mail: Johan.Elmberg@mna.hkr.se)*

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Dabbling ducks were studied on a eutrophic mid-flyway staging site in spring. Six species made up a temporary guild, in order of decreasing abundance they were: Teal (*Anas crecca*), Shoveler (*A. clypeata*), Mallard (*A. platyrhynchos*), Wigeon (*A. penelope*), Pintail (*A. acuta*), and Garganey (*A. querquedula*). Species richness and total abundance peaked around 20 April, whereas guild evenness was highest after the staging peak. Time use during the staging peak differed between the sexes in Mallard, but not in the other species. Mallard spent the least time foraging, whereas Shoveler and Teal foraged the most. Foraging behavior differed among species; i.e. Wigeon was mainly on land, Shoveler mainly fed from the water surface, whilst Mallard and Teal were more generalist. For the guild as a whole, shallow inshore areas were overused compared to offshore habitats. Microhabitat use of foraging birds differed among species; Pintail and Shoveler mainly fed in the offshore end of the habitat gradient, whereas Teal, Garganey, female Mallard, and especially Wigeon used shallow microhabitats. Teal and female Mallard had the highest overlap in microhabitat use, Shoveler and Wigeon had the least. Abundance of invertebrate prey was low during the staging peak, but increased sharply thereafter. This study indicates that eutrophic mid-flyway sites may offer less food to staging birds than do breeding lakes to which many of them are headed.

1. Introduction

Dabbling ducks (genus *Anas*) are among the most conspicuous inhabitants of wetland ecosystems in temperate areas of the Northern Hemisphere. They are very important game birds as well as in focus for habitat management and conservation efforts. Dabbling ducks have also long served as model organisms in population and community ecology (e.g. Trost *et al.* 1993, Nichols *et al.* 1995, Newton 1998, Johnson *et al.* 2002). However, despite a long research record there is still considerable disagreement to what extent local assemblages are structured by interspecific competition and by resource limitation (Nudds *et al.* 1994 *versus* Pöysä *et al.* 1996).

North American and European studies together provide a detailed picture of migratory and behavioral patterns of dabbling ducks (e.g. Batt *et al.* 1992, Scott & Rose 1996). Physiological adaptations for feeding, migration and reproduction are also fairly well documented (Batt *et al.* 1992). Population trends are known for many species (e.g. Delany & Scott 2002), but variation in vital rates in relation to population density is poorly known in most. Hence, it is generally unresolved what limits or regulates population size. Energy requirements and diet choice have been studied in several species and on different continents (e.g. Cramp & Simmons 1977, Batt *et al.* 1992, Tamisier & Dehorter 1999). Guild structure and niche separation have been described in numerous studies about time use and microhabitat choice, carried out in wintering (reviewed by Paulus 1988, with recent additions such as Guillemain *et al.* 2000b, c) as well as in breeding areas (North America: Dwyer 1975, Hickey & Titman 1983, Nudds 1983; Europe: Asplund 1981, Danell & Sjöberg 1982, Pöysä 1986, 1987, Mjelstad & Saetersdal 1988, Åström 1992, Nudds *et al.* 1994).

However, no scientific study has been published about time use, microhabitat use, foraging mode, or niche overlap in spring-staging dabbling ducks. This is remarkable considering the amount of research done about these birds in other seasons, and even more so because late spring is crucial to the build-up of lipid reserves used during migration and in the early stages of nesting (Swanson *et al.* 1985, Krapu & Reinecke 1992). Lipids together with proteins obtained on breeding lakes affect individual breeding success (Batt *et al.* 1992, but see Young 1993), a focal measure in evolutionary biology, in population ecology, and in waterfowl management (e.g. Batt *et al.* 1992). As many dabbling ducks are probably “income breeders” (i.e., relying solely on resources obtained on breeding grounds for egg formation and other reproductive energetic expenditure) rather than “capital breeders” (relying on stored reserves; Alisauskas & Ankney 1992, Young 1993, Jönsson 1997), studies of time use, foraging mode and microhabitat use at localities used the last weeks prior to arriving at breeding sites seem especially relevant and surprisingly lacking.

The present work was carried out at such a locality, a eutrophic mid-flyway wetland used by large numbers of spring-migrating staging ducks two to three weeks before their arrival at breeding grounds farther north and east. We thus studied a setting in which high dietary demands of ducks coincide with high local abundance in the guild; a situation for which general ecological theory predicts that resource limitation may lead to intraguild competition reducing niche overlap. We therefore addressed the following questions: (1) what is the pattern of time use in different species and sexes?, (2) what are the patterns in microhabitat use?, (3) is there niche segregation within the guild in terms of foraging behavior and microhabitat use?, (4) what and how much invertebrate prey is available?, and (5) is staging timed to a peak in invertebrate abundance?

2. Materials and methods

2.1. Study area

This study was done in the spring of 2001 in the province of Scania in southernmost Sweden, where all European species in the guild (i.e. *Anas acuta*, *A. clypeata*, *A. crecca*, *A. penelope*, *A. platyrhynchos*, *A. querquedula*, and *A. strepera*) may co-occur on single wetlands on spring migration. Ringing recoveries show that the study area is strategically situated mid-way within the major flyway connecting wintering areas in France, England, Belgium, and the Netherlands to breeding grounds in boreal Sweden, Finland and Russia (Koskimies 1956, Fransson & Pettersson 2001).

We used the Isternäset nature reserve in the outskirts of the city of Kristianstad (56°02’N, 14°09’E). Our study site is a mosaic of grazed meadows and very shallow wetlands, making up the north-eastern two-thirds of the reserve, i.e. 0.79 km^2 of level and low-lying land adjacent to the river Helge Å. Isternäset has long been a popular bird-watching site, why local phenology and annual occurrence of wetland birds are well documented (e.g. Ekberg & Nilsson 1994). The reserve is used by geese and ducks the year around, although it may be deserted for a few weeks in winter if ice forms. Mallard is the only regularly occurring dabbling duck in mid-winter. Isternäset is in

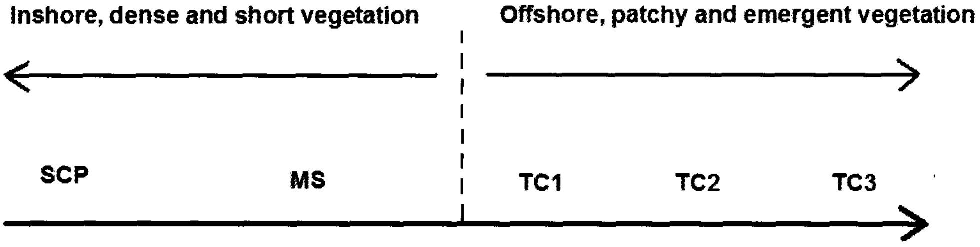

Fig. 1. The microhabitat gradient at Isternäset: SCP = "short *Carex* and *Poaceae*", MS = "muddy shore", TC = "tall *Carex*" in three categories ordered by increasing height and patchiness and decreasing overall density (TC 1 => TC2 => TC3). Out of the total hydrolittoral in area L, SCP made up 34.5%, MS 2.0%, TC1 38.0%, TC2 6.4%, and TC3 19.0%.

the nemoral biotic zone, but it is only some 15 kilometers south of the fairly steep transition to the hemi-boreal zone dominated by coniferous forest and average winter temperatures below 0°C.

We divided the study site into two parts; a larger and somewhat more distant area B (0.68 km^2) used only for abundance counts, and a smaller area L (0.11 km^2) where ducks were easily observed at close range (50–150 m) without being disturbed. Area L was used for abundance counts as well as for all behavioral studies. Water depth in most of areas B and L is less than 40 cm, being governed by the flow in Helge Å. Area L comprised five hydrolittoral microhabitat types. The shallowest was "short *Carex* and *Poaceae*" (SCP), a mix of heavily grazed meadow and scattered ungrazed low tussocks. Slightly deeper, but structurally the least complex microhabitat was "muddy shore" (MS) – basically very shallow water with a muddy bottom and few scattered non-emergent aquatic plants. The remainder was "tall *Carex*", but with considerable variation in patchiness and water depth. We therefore divided this type into three categories in order of increasing vegetation height, patchiness, and water depth (TC1->TC2->TC3). The gradient of microhabitat types is summarized in Fig. 1. They naturally divide area L into 40 patches, each of fairly homogeneous vegetation. Patches, tussocks, shoreline and other natural borders were combined with fence-posts into a reference system in which individual ducks could be assigned to a precise location and microhabitat. All fieldwork was done by CA.

2.2. Duck counts

All dabbling ducks in areas L and B were counted on 15 days during the spring staging period 1 April – 15 May (dates in Table 1). This was done in the morning on six days and in the evening on nine days. Ducks were counted before as well as after studying microhabitat use and time use, and the mean of the two abundance counts was used in subsequent analyses. Exceptions were 1, 4, and 29 April, when only one count was done. Counts and behavioral studies were made from two observation points overlooking the area; a road bank and an observation platform.

2.3. Time use and microhabitat use

On each study day roughly two hours were spent sampling time use and microhabitat use. Time use was recorded 50 times per sex and species on each study day. This was done in a consecutive manner going from one bird to the next, from left to right, and starting over from the far left individual when there were less than 50 of a certain species and sex (cf. Altman 1974). Sometimes a smaller sample was obtained because all ducks of a certain category left area L before a full count was obtained. Time use was assigned to one of seven categories: (1) sleeping, resting or vigilant, (2) swimming or walking without feeding (3a) foraging on land, (3b) foraging on the water surface, (3c) foraging with only the head under water, (3d) foraging with head and neck under water, (3e) foraging up-ending (classification follows Szijj 1965 and Pöysä

1986). Benefits, dangers and trade-offs of these behaviors have been discussed by Pöysä (1987, 1989) and by Guillemain *et al.* (2000a, b, c). Foraging birds in the time use study were assigned to one of the five microhabitat types described previously. Individuals that were not foraging, i.e. those with a behavior in category 1 or 2, were not included in the analyses of microhabitat use.

Every day some ducks were sampled more than once, as there were always less than 50 birds of each species and sex present in area L. However, the probability of sampling the same bird on more than one day was small: 1) Isternäset is centrally located in the flyway, and ducks are frequently seen departing for continued migration; 2) there was an exchange of staging birds between areas L and B, so that "unsampled" individuals from area B were likely to occur later in area L even if no new migrants had arrived; and 3) although there are no data about stop-over duration in spring-migrating dabbling ducks in Northern Europe, turnover was probably high at Isternäset. This assumption is supported by the fact that Green-winged Teal (*Anas crecca carolinensis)*, a vagrant from North America occurring singly in flocks of spring-migrating "Eurasian" Teal, remain on average only three days (median 2 days) when on staging sites in southern Sweden in April (n = 12 *carolinensis* drakes, data from 1984–1998 from the provinces of Scania and Halland supplied by the Swedish Ornithological Rarities Committee). As these birds occur together with staging long-distance migrating "Eurasian" Teal they can be assumed to share the migration schedule of the latter. Hence, we treat each individual on each day as a new sample in our analyses of time use and microhabitat use, but we acknowledge the possibility that single birds, especially Mallards in May, might have been included more than once.

We focus the analyses of time use and microhabitat use on the staging peak period by including data from April only (four morning and four evening counts = 16 hours of observation). Mallard, however, occurred in similar numbers throughout the entire study, permitting an intraspecific comparison of time and microhabitat use between the staging peak and the post-peak time period. Staging Pintail and Garganey were so few that they were not included in tests and conclusions, but due to the total lack of published spring data for these species we present the descriptive results obtained (Figs. 4, 5).

Interspecific differences in time use were explored by pair-wise contrasts involving all species with more than ten sampled individuals. For this analysis we pooled data from males and females (cf. Table 2), but in Mallard sexes were considered separately because of the intersexual difference in time use. Virtually all ducks except Mallard occurred in pairs, with male and female only meters apart. This was expected considering that pairing generally occurs already in fall and winter in dabbling ducks (Cramp & Simmons 1977, Glutz von Blotzheim 1989, Guillemain *et al.* 2003). Microhabitat use was thus expected to differ between sexes in Mallard only. Difference in microhabitat use among the other species was tested using male data only, as female data were assumed to be dependent of the former. As in the analysis of time use, Pintail and Garganey were excluded from statistical testing because of the low number of individuals involved (see results).

2.4. Food abundance

Nektonic and benthic invertebrates are preferred prey to most dabbling ducks, especially in spring and in early summer in response to increased nutritional demands for migration and breeding (Batt *et al.* 1992). Invertebrates were sampled at Isternäset weekly 17 April–13 May, using 9 – 11 one liter activity traps (procedure described in Elmberg *et al.* 1993) placed horizontally on the bottom in the shallow littoral zone of area L for 24 hours. Placement depth of traps ranged from 5 cm to 40 cm to cover the range of feeding depths of dabbling ducks. Half of the traps were placed in dense vegetation (microhabitat SCP; cf. Nummi 1993) and the other half in more open vegetation of intermediate density (microhabitat type TC2 or TC3). At emptying, the contents of each trap were passed through a one mm mesh sieve. Remaining animals were preserved and later counted in the laboratory. The catch from each trap was analysed separately, and invertebrates were classified according to Table 2 in Nudds and Bowlby (1984) with the correction of Elmberg *et al.* (1993) due to size differences between North America and Northern Europe in some taxonomic groups. For each sam-

Table 1. Daily abundance of dabbling ducks at Isternäset 1 April–15 May 2001 (areas L and B combined). Except for 1, 4, and 29 April, all numbers are a mean of two counts, conducted before and after time use and microhabitat use were studied. Σ is the total number of dabbling ducks, S is species richness, and E is evenness of the guild.

Species	**Sex**	**1** April	**4** April	**17** April	**20** April	**22** April	**25** April	**27** April	**29** April	**1** May	**4** May	**6** May	**8** May	**11** May	**13** May	**15** May
Mallard	M	8.0	12.5	4.5	4.5	6.0	6.5	7.0	7.5	8.0	8.0	12.5	13.0	9.5	4.5	16.5
	F	4.0	4.0	0.5	1.0	0.5	2.0	5.0	3.0	1.5	1.5	3.0	4.5	2.0	2.5	4.5
Teal	M	65.0	63.0	63.5	61.5	55.5	58.5	54.5	40.5	21.5	5.5	2.0	5.0	0.5	0.0	0.0
	F	56.0	54.5	54.0	47.5	45.5	55.0	44.5	36.5	13.5	5.0	2.0	2.5	0.0	0.0	0.0
Shoveler	M	1.0	16.5	14.0	18.5	12.5	23.0	13.5	13.0	19.5	17.5	4.5	2.0	5.0	5.0	2.0
	F	0.0	13.0	13.5	18.5	9.5	11.5	7.5	5.0	7.5	8.0	2.0	1.0	1.5	0.5	1.0
Pintail	M	4.0	1.5	1.5	1.0	1.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	F	1.0	1.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Wigeon	M	3.0	0.0	3.5	1.0	3.0	5.0	11.5	3.5	6.0	5.0	3.0	3.5	1.5	0.5	0.0
	F	3.0	0.0	2.5	1.0	2.0	4.0	5.5	2.5	4.0	2.5	3.0	3.0	1.0	0.0	0.0
Garganey	M	0.0	2.0	0.0	0.5	0.5	1.5	0.5	0.0	2.0	0.0	1.5	1.0	0.0	0.5	2.5
	F	0.0	1.0	0.0	0.5	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.5	0.0	0.0	0.0
Σ		**145.0**	**169.5**	**158.0**	**155.5**	**136.0**	**167.0**	**149.5**	**112**	**84.0**	**53.0**	**33.5**	**36.0**	**21.0**	**13.5**	**26.5**
S		**5**	**5**	**5**	**6**	**6**	**5**	**5**	**5**	**5**	**4**	**5**	**5**	**4**	**4**	**3**
E		**0.28**	**0.38**	**0.34**	**0.30**	**0.29**	**0.39**	**0.42**	**0.39**	**0.66**	**0.77**	**0.67**	**0.62**	**0.61**	**0.57**	**0.51**

pling occasion, mean catch per trap was also divided by the number of dabbling ducks present in the entire study area in order to obtain a relative measure of per capita prey abundance (Fig. 2). No weighting by prey size was used to obtain this index, as the size class distribution of prey animals was very similar throughout the study.

To get a basic picture of the availability of seeds as food, eight sites in the littoral were sampled in mid-April with a 1 mm-mesh pasta strainer dragged through the vegetation and the upper bottom layer in microhabitats TC1, TC2, and SCP of area L. However, no seeds at all were found.

2.5. Statistics and formulas

All tests were run with the SPSS 11.0 software. All probabilities are two-tailed. Evenness was calculated using the formula: $E = D/D\ \mathrm{max} = 1/((S)*\Sigma pi^2)$. We used Horn's index of overlap (cf. Krebs 1999) to calculate similarity in microhabitat use between species.

3. Results

3.1. Duck counts

All European species in the guild except Gadwall were observed during the study (Table 1). Daily species richness peaked at six on 20–22 April, and five species or more were observed on 11 days out of 15. Teal and Shoveler were the most abundant species, both having a prolonged staging peak in mid-April (Table 1, Fig. 2). Mallard was less abundant, but occurred in fairly stable numbers throughout. Wigeon was scarcer than Mallard, though it was present for most of the study period. Pintail and Garganey both occurred in very low numbers, the former early, the latter throughout. Guild composition thus differed markedly between the first and the second half of the study. Evenness was stable but fairly low in April, much higher in May (Table 1).

Pooling daily abundance data for all species in the guild showed that the shallower and more inshore area L was preferred, i.e. over-used, com-

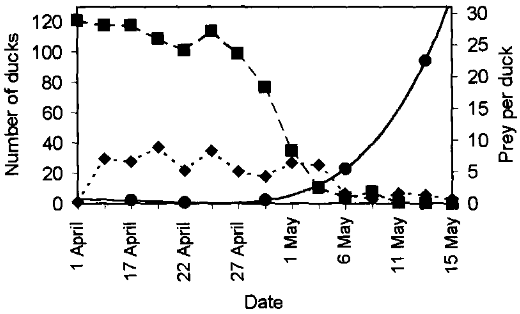

Fig. 2. Abundance of Teal (squares) and Shoveler (diamonds) at Isternäset in the spring of 2001. Prey per duck (dots) is a per capita index, i.e. the abundance of invertebrate prey per dabbling duck (see Results for further definitions and prey trapping details), and it was fitted by a 6th order polynomial tendency curve.

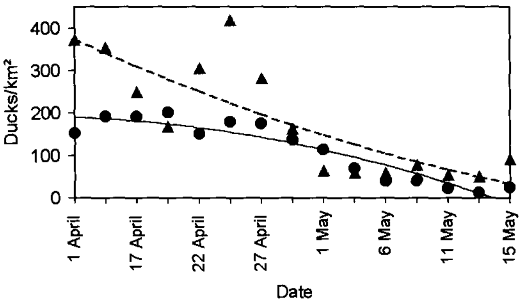

Fig. 3. Pooled densities of dabbling ducks revealed an over-use of the shallower more inshore area L (triangles) compared with the adjacent, deeper and more offshore area B (dots), especially during the staging peak in April. Values for the different areas were fitted by a second order polynomial (area L dashed, area B solid line).

pared with the adjacent larger, partly deeper, and more offshore area B during the staging peak in April (Fig. 3). However, in May when mainly local breeders remained on the site, both areas had similar densities of dabbling ducks. Mallard was the only species to hatch broods during the study (the first sighted on 11 May), but several Shoveler broods appeared after fieldwork was concluded.

3.2. Time use and microhabitat use

Time use did not differ significantly between sexes in three of the four species with a fair sample size (Fig. 4; likelihood ratio test: P > 0.20 in Shoveler, Teal and Wigeon; sample size is the number of observations in Table 2). Female Mallards, though, spent more than twice as much time feeding than did males, and the former also used the entire feeding depth gradient more evenly (Fig. 4). This be-

Table 2. Sample size in behavioral studies of sympatric dabbling ducks during the staging peak in April. "Mallard late" denotes data from 6–15 May, i.e. after the staging peak of congeneric species. The number of individuals in the microhabitat study is lower because only foraging birds were included.

Species	Sex	Sampled individuals	Time use study; number of observations	Microhabitat use study; number of observations
Pintail	M	4	146	88
	F	2	55	8
Shoveler	M	19	300	232
	F	16	300	238
Teal	M	85	397	318
	F	68	397	331
Wigeon	M	8	152	95
	F	6	152	101
Garganey	M	3	48	34
	F	1	21	16
Mallard	M	4	370	54
	F	11	233	121
Mallard, late	M	22	250	71
	F	7	200	123

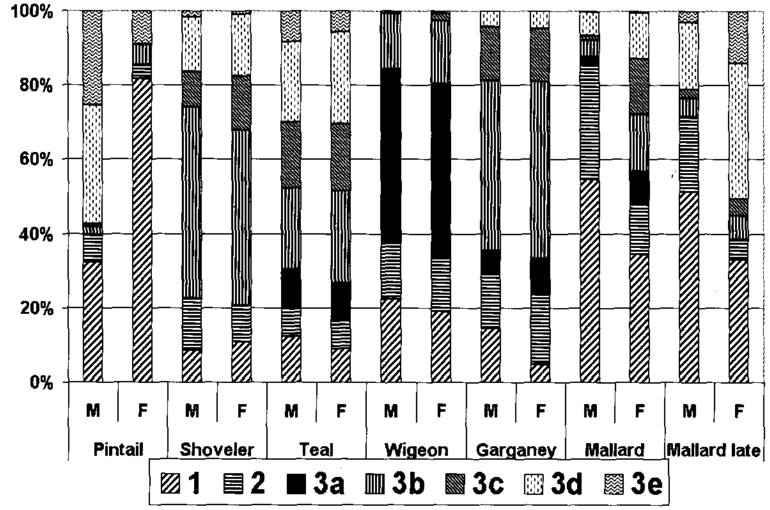

Fig. 4. Time use in male (M) and female (F) sympatric dabbling ducks during the staging peak in April. "Mallard late" denotes data from 6–15 May, i.e. after the staging peak of congeneric species. The sampling unit was observation (Table 2). Time use categories: (1) sleeping, resting or vigilant, (2) swimming or walking without feeding, (3a) foraging on land, (3b) foraging on the water surface, (3c) foraging with head only under water, (3d) foraging with head and neck under water, (3e) foraging up-ending.

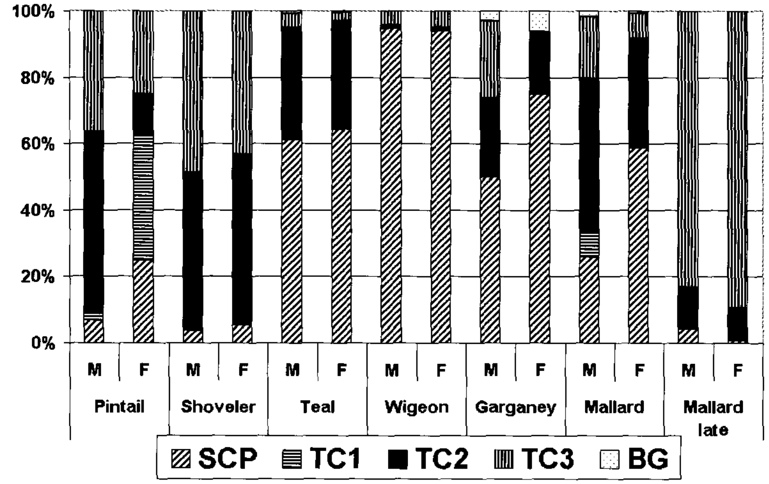

Fig. 5. Microhabitat use in foraging male (M) and female (F) sympatric dabbling ducks during the staging peak in April. "Mallard late" denotes data from 6–15 May, i.e. after the staging peak of congeneric species. The sampling unit was observation (Table 2). Microhabitat acronyms and definitions are given in Fig. 1 and in Methods.

havioral difference was obvious in the field, and highly significant as revealed by the likelihood ratio test ($P < 0.001$, sample sizes in Table 2). By and large, interspecific differences in time use were considerable. Shoveler, Teal, Wigeon, male Mallard, and female Mallard all differed significantly from each other in time use (nine pair-wise likelihood ratio tests; $P < 0.001$ in all cases, sample sizes for different species is the number of observations in Table 2). Mallards of both sexes spent the least time foraging, whereas Shoveler and Teal foraged the most. Foraging behavior proper differed among species, i.e. Wigeon did most of it on land,

Table 3. Pooled microhabitat use of foraging dabbling ducks during the staging peak. Expected use was calculated from 1830 observations of six species of ducks assuming that each microhabitat would be used in proportion to its area.

Microhabitat type	**Expected use**	**Observed use**
Short *Carex* and *Poaceae* (SCP)	632	741
Muddy shore (MS)	38	8
Tall *Carex* 1 (TC1)	695	10
Tall *Carex* 2 (TC2)	117	594
Tall *Carex* 3 (TC3)	348	477

Table 4. Pair-wise tests of microhabitat use in foraging dabbling ducks during the staging peak. Shoveler, Teal, and Wigeon are represented by data from males only. Sample sizes are found in table 2, and include the number of individuals involved as well as the number of observations on which the test was based. Maximum degree of freedom is 4; i.e., when at least one of the species in the pair-wise test occurred in all five habitats. Below the diagonal is the likelihood ratio test statistic.

Species	Shoveler	Teal	Wigeon	Mallard male	Mallard female
Shoveler		P < 0.001 df = 3	P < 0.001 df = 2	P < 0.001 df = 4	P < 0.001 df = 4
Teal	286		P < 0.001 df = 3	P < 0.001 df = 4	P = 0.380 df = 4
Wigeon	287	60		P < 0.001 df = 4	P < 0.001 df = 4
Mallard male	47	41	88		P < 0.001 df = 4

Table 5. Species-pair overlap (Horn's index) in microhabitat use in foraging dabbling ducks during the staging peak. Sample size is the number of observations for each species in Table 2.

Species	Teal	Wigeon	Mallard male	Mallard female
Shoveler	0.613	0.283	0.851	0.671
Teal		0.836	0.854	0.990
Wigeon			0.571	0.826
Mallard male			0.903	

Shoveler fed mainly from the water surface, while Teal and Mallard were more diverse in foraging mode.

In mid-May, after the staging peak and when Isternäset hosted far fewer dabbling ducks, male Mallards still spent much less time feeding than did females (Fig. 4, Table 1). Moreover, both sexes showed a significant change in time use from April to early May, spending more time feeding and shifting to foraging deeper in the water column in the latter period (Fig. 4; likelihood ratio test: $P < 0.001$ in both sexes, sample sizes in Table 2).

Microhabitat use in the foraging guild as a whole (data for all species pooled) was very selective during the staging peak in April; i.e. microhabitats were not used in proportion to their area (χ^2: 2700; df = 4, $P < 0.0001$; Table 3). Preference was strongest for "tall *Carex* 2", being used four times as much as expected, whereas "tall *Carex* 1" and "muddy shore" were clearly under-used. Specific patterns differed strikingly (Fig. 5); Pintail and Shoveler foraged in the offshore end of the habitat gradient (cf. Fig. 1), whereas Teal, Garganey, female Mallard and especially Wigeon did so in the shallower end. All pair-wise contrasts except for that between Teal and female Mallard were significant (Table 4). Note that male and female Mallard again differed significantly, mainly in the use of shallow grazed habitats (SCP). Teal and Mallard females were the most similar with respect to microhabitat use, whereas Shoveler and Wigeon were the least similar (Table 5). Other species pairs with little overlap were Wigeon – male Mallard and Shoveler – Teal. Interspecific aggression was never observed during the study, but intraspecific aggression was frequent among Shovelers and Mallards.

Mallards of both sexes changed their pattern of microhabitat use from April to early May, primarily by leaving shallow foraging areas in favor of the most offshore areas (Fig. 5; likelihood ratio test: $P < 0.001$ in both sexes, sample sizes in Table 2).

3.3. Food abundance

Invertebrate abundance was low in April, but increased sharply in early May (Table 6). The smallest prey size class (i.e., 1–2.5 mm) dominated the catch throughout. *Copepoda* was the most abundant prey group (72% by numbers), followed by *Coleoptera* (adult and larvae) (15%), *Ostracoda*

Table 6. Abundance and size distribution of invertebrate prey in activity traps at Isternäset in 2001. Sampling procedures are detailed in "Materials and methods".

Date Number of traps	**17 April** 9	**22 April** 11	**29 April** 11	**6 May** 11	**13 May** 10
Length category					
1 (1–2.5 mm)	562	187	440	1,658	2,476
2 (2.6–7.5 mm)	21	19	9	12	11
3 (7.6–12.5 mm)	55	34	23	101	102
4 (12.6–20.0 mm)	49	30	144	260	448
Total	686	269	615	2,031	3,035
Abundance/trap	**76.3**	**24.5**	**56**	**184.6**	**303.7**

(7%), *Acari* (3%), and *Isopoda* (2%). No energetic analysis of prey animals was done, but based on previous studies of size and caloric density (e.g. references in Nudds & Bowlby 1984), we estimate that *Coleoptera*, *Isopoda* and *Copepoda* were the energetically most important prey groups, respectively.

4. Discussion

It is evident that we studied a temporary guild mainly comprising transient birds. Probably all Teal, Wigeon, and Pintail, as well as many Shoveler were on their way to breeding grounds farther north and east. The first three species are extremely rare as breeders in the study area (Ekberg & Nilsson 1994). Mallard numbers, though, were fairly constant, implying that many of those birds were residents. This species arrives at boreal breeding grounds 1,000 km farther north in Sweden already in mid-April (e.g. Olsson & Wiklund 1999), hence our study was done after the main passage of boreal Mallards.

During the staging peak in April, Shoveler, Teal, and Wigeon spent less time loafing and resting, and more time feeding than they do on their winter quarters (Paulus 1988, Rave & Baldassarre 1989). Male Mallards at Isternäset had a time budget similar to that of males on wintering sites, i.e. most of the time was spent not feeding. Female Mallards, on the other hand, spent less time resting and more time feeding than they do in winter. In Shoveler, Teal, and Wigeon the time spent resting was less than 25% in both sexes. In other words, most of the time was used for feeding or for locating good foraging patches. All these observations fit well with expectations derived from energy requirements connected with migration and egg formation (Batt *et al.* 1992), especially if Shoveler, Teal, and Wigeon were mainly transient birds, and many Mallards were local breeders.

When patterns of foraging mode, feeding depth, and microhabitat use are combined, Teal, Wigeon, Shoveler, and Mallard separate remarkably well into the niches to which they are traditionally ascribed on breeding and wintering sites throughout the Holarctic (e.g. Pöysä 1986, Nudds 1992, Nudds *et al.* 1994, Nummi *et al.* 1994, Tamisier & Dehorter 1999, Nummi & Väänänen 2001). Pintail and Garganey were few in this study, but their behavior too conformed with known patterns, i.e. Pintails were in the offshore areas alongside Shovelers but foraged much deeper, and Garganeys had much the same microhabitat use as Teal, but tended to forage shallower.

Spring staging of dabbling ducks was obviously not timed to a general peak in invertebrate abundance. If anything, most transient birds left Isternäset prior to the increase in invertebrate abundance. Very little is published, from Fennoscandia and elsewhere, about the relative availability of food on spring staging sites as compared with breeding lakes to which the birds are headed. Invertebrate abundance in this study (17, 22, and 29 April) was somewhat higher than May values from boreal breeding lakes in Fennsocandia (mean = 21 prey items / trap, n = 580 activity traps from 29 lakes; Elmberg, Nummi, Pöysä and Sjöberg, unpublished data). However, if only prey >2.5 mm are considered (size classes 2–4 in table 6), means at Isternäset are only half of those found at oligotrophic breeding lakes a few weeks later in the season. This comparison concerns raw trap means, i.e. numbers have not been adjusted for density of foraging ducks. If this were done, per capita prey availability at Isternäset during the staging peak would probably come out significantly lower than that later encountered at arrival on boreal breeding lakes.

Dabblings ducks generally eat a lot of plant material in fall and winter (e.g. Madsen 1988, Tamisier & Dehorter 1999, Guillemain *et al.* 2000 b,c). Plants are thus a potential alternative food resource if invertebrates are scarce. However, seed reserves were totally depleted in the Isternäset littoral (cf. Madsen 1988), and very few fresh sprouts from the aquatic vegetation were available during the staging peak. Sprouting terrestrial grass was abundant, though, and Teal, Garganey and Mallard females were observed to eat of it or among it to some extent.

Our study indicates that northbound dabbling ducks arriving in April at Isternäset, which is a genuinely eutrophic site, have less high-protein food available than they will have on typical oligotrophic boreal breeding lakes at which they arrive a few weeks later. Such a pattern, if general, will have profound impact on the pre-breeding build-up of fat and proteins, as well as on the migratory strategy adopted (cf. Alisauskas & Ankney 1992, Weber *et al.* 1998). Sjöberg's and Danell's (1982) study of a boreal Swedish breeding lake shows that the timing of nesting and subsequent hatching may be highly synchronized with a peak in chironomid emergence. Hence, the annual program of migration and breeding is a strategy of multiple trade-offs, and we can not expect birds to be at every site when local conditions are optimal. If anything, at least income breeders may benefit more from timing their migration primarily to the temporal pattern of food abundance on breeding grounds.

In Mallards of both sexes there was a shift in feeding behavior and microhabitat use as invertebrates became more abundant in May. However, cause and effect are unclear; the change to foraging more in deeper offshore waters can also be regarded as a niche expansion related to the departure of potentially competing congeners. Such a shift, but in the opposite direction, was observed on a breeding lake within the same flyway by Pöysä (1986), who found that Mallards foraged deeper in the presence of Teal than in their absence. Hence, foraging niche shifts in Mallard may be due to density dependent processes, rather than being a species-specific tracking of changes in prey abundance or composition. There may also be costs to foraging deeper, as vigilance decreases and predation risk may increase (Guillemain *et al.* 2000a, 2001, Pöysä 1987, 1989).

As there is no study of spring-staging dabbling ducks to compare with, the generality of the present results is unclear. Depending on whether spring staging sites are hypothesized to offer more or less food than wintering and breeding areas, predictions about competition and niche overlap on the former will differ. The conventional wisdom among conservationists in Europe has long been that spring staging sites like Isternäset offer an abundance of food and that they constitute important "feeding stations" on which migration as well as subsequent breeding success depend. Invertebrate abundance patterns and duck behavior in the present study indicate the opposite, i.e. that dabbling ducks find limited amounts of food at this eutrophic staging site. Resource limitation may thus prevent competitive release, relating to the observation that niche adherence was more pronounced in this study than it is on some wintering areas within the same flyway (Tamisier & Dehorter 1999).

Apart from challenging the generality of the patterns found in this study, future work needs to focus on staging sites closer still to the breeding areas, e.g. on boreal estuaries and coastal wetlands where ducks spend the last week or days before arriving at their breeding lakes. The former may offer more food than "mid-trip" sites like Isternäset, and they may also play a significant role in the build-up of resources for egg formation. We also need a deeper understanding of food depletion patterns in sites like Isternäset. Do seeds run out in late winter or already in fall (cf. Madsen 1988), and when, if at all, does protein-rich invertebrate food contribute significantly to energy budgets of staging ducks?

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Tidsbudget, födosöksbeteende och mikrohabitatanvändning i ett temporärt simandsgille på en vårrastlokal

På en näringsrik vårrastlokal studerade vi ett temporärt "gille" av sex simandsarter, vilka ordnade efter avtagande abundans var: kricka (*Anas crecca*), skedand (*A. clypeata*), gräsand (*A. platyrhynchos*), bläsand (*A. penelope*), stjärtand (*A. acuta*) och årta (*A. querquedula*). Såväl gillets artantal som dess totala individrikedom var högst kring 20 april. Kricka och skedand var överlag de talrikaste arterna, men deras dominans i gillet minskade efter detta datum. Under rastningstoppen skilde sig tidsanvändningen mellan könen hos gräsand, men inte hos de andra arterna. Skedand och kricka ägnade mest tid åt födosök, gräsanden minst. Födosöksbeteendet var mest specialiserat hos bläsand (bete på land) och skedand (filtrering i vattenytan), medan kricka och gräsand var generalister som sökte föda både på land, på vattenytan och på bottnar av olika djup. Gillet som helhet överutnyttjade grunda strandnära habitat.

Mikrohabitatutnyttjandet skilde sig mellan arterna: stjärtand och skedand sökte huvudsakligen föda i öppna djupa partier, medan kricka, årta, gräsandshonor och särskilt bläsand utnyttjade grunda mikrohabitat. Kricka och gräsandshonor hade störst överlappning i mikrohabitatutnyttjande, skedand och bläsand minst. Mängden tillgänglig evertebratföda var låg under ändernas rastningstopp, men ökade kraftigt därefter. Studien antyder att simänder på produktiva lokaler halvvägs längs sin vårflyttning kan ha mindre tillgång till evertebratföda än på de ofta mer oligotrofa lokaler längre norrut där de rastar och häckar.

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