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Time use and foraging behaviour in pre-breeding dabbling ducks *Anas* spp. in sub-arctic Norway

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Abstract We studied time budgets and foraging methods in pre-breeding Mallard *Anas platyrhynchos*, (Eurasian) Teal *Anas crecca*, Wigeon *Anas penelope*, Pintail *Anas acuta*, Shoveler *Anas clypeata* and Gadwall *Anas strepera* in subarctic Norway in May. Among all six species studied, foraging accounted for the most common use of time, ranging from 19 % in male Pintail to 40–60 % in female Mallard, Teal, Pintail and Gadwall. Comfort behaviours amounted to 20–34 % of the time budget, and interaction and disturbance were marginal. Vigilance time ranged from 8 % in female Mallard to 20 % in male Pintail. Movement amounted to some 20 % of the time in most species and sexes. In Wigeon, sexes did not differ in time use, whereas in Mallard, Pintail and, in particular, Teal, females foraged more and engaged less in vigilance and interactions than did males. In addition, Teal and Mallard males engaged in the riskier foraging methods less than females, but more in those permitting vigilance. Although overlap in feeding methods was large among these species, Mallard and Teal were generalists, feeding at all depths, Wigeon foraged mainly in shallow water and Pintail foraged essentially in deep water. Our results support the income/capital breeder hypothesis with respect to males only; compared to lighter species, heavier species allocated less time to foraging but

more to vigilance. We found no support for the hypothesis that long-distance migrants forage more to compensate for energy loss due to migratory flight. Foraging time in females was related to breeding phenology; early nesters spent more time feeding than later nesters.

Keywords Time budget · Foraging method · Anatinae · Spring · Stopover · Sex difference

Zusammenfassung

Aktivitätsbudgets und Verhaltensweisen der Nahrungssuche bei Gründelenten der Gattung *Anas* vor der Brutzeit im subarktischen Norwegen

Wir untersuchten Zeitbudgets und Methoden des Nahrungserwerbs bei Stockente *Anas platyrhynchos*, Krickente *Anas crecca*, Pfeifente *Anas penelope*, Spießente *Anas acuta*, Löffelente *Anas clypeata* und Schnatterente *Anas strepera* im Mai vor Beginn der Brutzeit im subarktischen Norwegen. Die meiste Zeit wurde für die Nahrungssuche verwendet; anteilig zwischen 19 % bei männlichen Spießenten bis hin zu 40–60 % bei den Weibchen von Stock-, Krick-, Spieß- und Schnatterente. Der Anteil des Komfortverhaltens betrug 20–34 %, Interaktionen und Störungen traten nur in geringem Maße auf. Wachsamkeitsverhalten nahm zwischen 8 % der Zeit bei Stockentenweibchen und 20 % der Zeit bei Spießerpeln ein. Fortbewegung beanspruchte etwa 20 % der Zeit bei beiden Geschlechtern der meisten Arten. Bei Pfeifenten gab es keine Geschlechtsunterschiede in den Aktivitätsbudgets, wohingegen die Weibchen von Stockente, Spießente und insbesondere Krickente mehr nach Nahrung suchten und weniger an Wachsamkeit und Interaktionen teilhatten als die Männchen. Außerdem nutzen Krick- und

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Stockentenmännchen bei der Futtersuche im Vergleich zu den Weibchen seltener riskantere Methoden und dafür eher solche, die eine gleichzeitige Wachsamkeit erlaubten. Obgleich die Methoden des Nahrungserwerbs sich zwischen den Arten stark überschneiden, traten Stock- und Krickenten als Generalisten auf, die alle Wassertiefen nutzten, Pfeifenten fanden hauptsächlich in seichtem Wasser ihr Futter, und Spießenten suchten primär in tiefem Wasser nach Nahrung. Unsere Ergebnisse betätigten die „Income-Capital-Breeder“-Hypothese nur in Bezug auf die Männchen; schwerere Arten verbrachten im Vergleich zu leichteren weniger Zeit mit dem Nahrungserwerb als mit Wachsamkeit. Wir fanden dagegen keine Bestätigung der Hypothese, dass Langstreckenzieher mehr nach Futter suchen, um durch den Zug bedingte Energieverluste auszugleichen. Bei den Weibchen hing die mit Nahrungserwerb verbrachte Zeitspanne mit der Brutphänologie zusammen; früh nistende Weibchen verbrachten mehr Zeit auf die Futtersuche als später brütende.

Introduction

How environmental conditions encountered during the spring migration affect subsequent breeding performance is a key issue in conservation and management programs which focus on migratory birds, not least in those nesting at high latitudes (e.g., Kostin and Mooij 1995; Morrison et al. 2005). Nutrient acquisition during the spring migration is crucial to sustain migration and to a varying degree to prepare for subsequent reproduction (e.g. Madsen 2001; Drent et al. 2006).

There are many examples in the literature on waterfowl of behaviour during the pre-nesting period having general and profound effects on subsequent breeding success and survival (e.g. Ankney and MacInnes 1978; Ebbinge et al. 1982; Hepp 1984; Hohman et al. 1988; Zimin et al. 2002; Spaans et al. 2007). Yet, very little is still known about the spring migration ecology of dabbling ducks (Arzel et al. 2006, 2007; Pearse et al. 2011), and only a mere handful of studies have been carried out at the sites used during the final part of spring migration or have focused on birds freshly arrived at breeding grounds (Esler and Grand 1994; Paquette and Ankney 1998; MacCluskie and Sedinger 2000; Arzel et al. 2006, 2007). Spring-migrating dabbling ducks need to recuperate and replenish energy stores during and after their northward migration journey. Males additionally have to defend pair bonds and be vigilant against predators to enable their mate to maintain foraging time or use riskier foraging methods (Paulus 1983; Guillemain et al. 2007b). Females, on the other hand, need to

prepare for egg formation and incubation, both of which are energetically very costly (Swanson et al. 1985; Krapu and Reinecke 1992; Esler and Grand 1994). Behavioural differences between males and females are thus expected to occur in spring.

Nutrient requirements in spring and before nesting may not only differ between sexes but also depend on the physiological capacity to store energy in the first place (income vs. capital breeders: Jönsson 1997; Van der Meer and Piersma 1994; Klaassen 2002), migration strategy (short- vs. long-distance migrants) and breeding phenology (early vs. late nesters) (Berthold 2001; Newton 2008). The classical view is that larger bodied birds are able to store relatively more than smaller ones, permitting them to arrive with higher energy reserves on the breeding sites. In general terms, species which have both a long migratory journey and early nesting call for a faster replenishment of stores as breeding grounds are approached, as compared with species taking a shorter flight and/or more time until nesting starts. As metabolic changes associated with breeding are expensive in terms of energy, early breeders are expected to forage more than later breeders.

There is a need for studies of foraging patterns and time use in dabbling ducks at sites close to high-latitude breeding quarters. Links between spring conditions and subsequent reproductive success are also of interest in the context of climate change (Møller et al. 2010). Temperature rise and associated cascade effects on resource availability (e.g. mismatch scenarios) are among such postulated effects, which may become especially prominent at high latitudes (Guillemain et al. 2013).

Here we provide the first description of time-use patterns in a guild of migratory dabbling ducks in a subarctic area based on our observations on birds freshly arrived after the migration journey and immediately before breeding. We use our data to test the following predictions related to previous findings and hypotheses mentioned above: (1) females in all species should forage more than males; (2) males should devote more time to vigilance, interactions and aggression than females; (3) males should engage more than females in foraging methods which allow vigilance, i.e. foraging more often at or close to the water surface; (4) small-bodied species should use more time foraging than large-bodied species due to their relatively lower capacity to store energy; (5) long-distance migrants should forage more than short-distance migrants because the former have more depleted energy stores; (6) early nesters should forage more than late nesters due to breeding costs, in particular due to the more immediate needs for females to produce eggs.

Materials and methods

Study area

The study was carried out on Andøya (69°N, 16°E; Fig. 1), an island located in the northernmost part of Nordland county in Norway and situated literally at 'the northern end' of the European continent. Andøya is roughly 45 by 10 km (area 489 km²) and is covered mainly by barren mountains (altitude up to 705 m a.s.l.) and low-altitude treeless peat bogs. The latter, as well as a narrow coastal strip of farmland, is dotted with oligo- to mesotrophic wetlands that attract breeding waterfowl in summer. Andøya's climate is subarctic, with a cool growing season lasting from May to October and a mean temperature peaking at 11 °C in July.

Study species

Seven species of dabbling duck breed in northern Norway: Mallard *Anas platyrhynchos*, Pintail *Anas acuta*, Eurasian/Common Teal *Anas crecca*, Eurasian Wigeon *Anas penelope*, Gadwall *Anas strepera*, Garganey *Anas querquedula* and (Northern) Shoveler *Anas clypeata*. With the exception of a few wintering Mallard individuals, all birds migrate comparatively long distances in the spring to reach northern Norway (Bakken et al. 2003). The birds of these seven species which are found in northern Norway are among the most northerly breeders and those which migrate the farthest. As a consequence, they have a comparatively 'narrow time window' available for breeding and moult compared to conspecifics breeding in climatically more benign areas. All seven species are geographically wide-ranging in Europe and beyond.

On Andøya, as in other sub-arctic areas in the Palearctic, Mallard, Teal and Wigeon are widespread and common breeders (Cramp and Simmons 1977; Hagemeyer and Blair 1997). Pintail is a scarce but regular breeder, and some of the world's northernmost breeding Shoveler, Garganey, and Gadwall occur on Andøya and adjacent islands (Gjershaug et al. 1994). There are no comparative data on local breeding phenology, but in general terms the northern Fennoscandia Mallard is the earliest breeder in the guild, followed by Pintail, then Teal, and later by Wigeon, Shoveler and Gadwall (Table 1). Ringing recoveries show that most dabbling ducks occurring in the spring on Andøya are local or at least regional Norwegian breeders (Bakken et al. 2003).

Study period and weather

This study was carried out on Andøya 7–14 May 2008. Consequently, the ducks observed were either local breeders about to disperse to nesting ponds as soon as ice conditions permitted, or staging birds that still had to complete the final leg of their migration. Data from local ornithologists verify that our sampling period covered the major first influx in the spring of 2008 of all dabbling ducks except Mallard, of which a few hundred regularly winter in the area (Anette Jensen, personal communication). We observed flocks of Teal and Wigeon as they arrived on Andøya over the open ocean from the southwest. Most wetlands on Andøya were still covered in ice during our study, including all but a very few inland breeding ponds. Dabbling ducks thus essentially utilized coastal sites (cf. Tombre et al. 2005), which made them easy to find. Accordingly, we were able to sample all relevant sites on

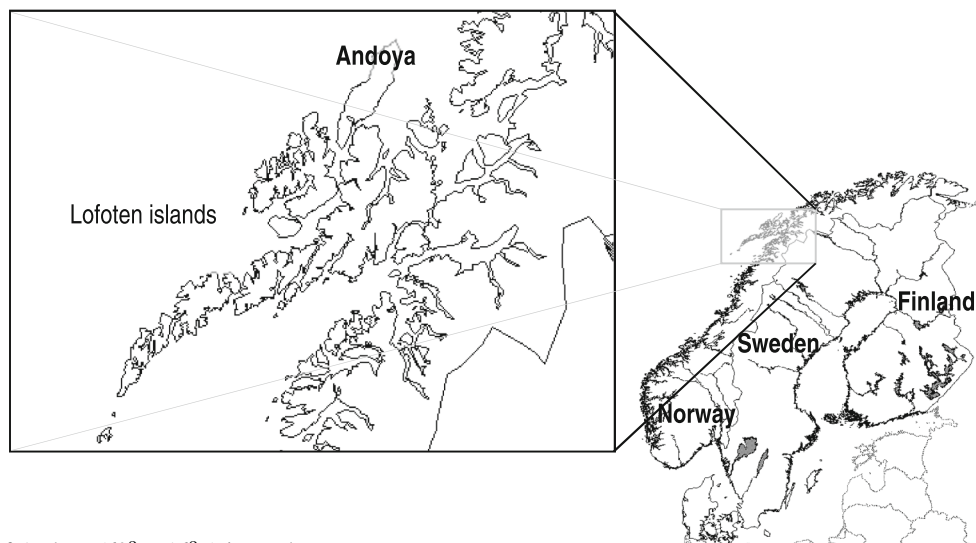


Fig. 1 Location of Andøya (69°N, 16°E) in northern Norway

Table 1 Body mass, migration distance and nest initiation order of dabbling ducks *Anas spp.* studied on Andøya, northern Norway

Species	Mean body mass (g)		Migration distance (km) ^a	Nest initiation order (rank) ^b
	Males	Females		
Mallard <i>Anas platyrhynchos</i>	1,100	900	1,000	1
Pintail <i>Anas acuta</i>	900	750	3,000	2
Gadwall <i>Anas strepera</i>	800	640	2,100	4
Wigeon <i>Anas penelope</i>	750	640	2,300	4
Shoveler <i>Anas clypeata</i>	650	550	2,700	4
Teal <i>Anas crecca</i>	350	285	2,000	3

Weight and migration distance values are based on Newton and Campbell (1975), Cramp and Simmons (1977), Scott and Rose (1996), Fransson and Pettersson (2001), Wernham et al. (2002), Bakken et al. (2003) and Fouque et al. (2004). Nest initiation order is based on a large number of published and unpublished sources, and the only unresolved ranking (Teal vs. Pintail) was settled by a questionnaire sent out to colleagues in waterfowl research (see "Acknowledgements")

^a Migration distance is the distance from the centre of the winter range to the study area

^b Nest initiation order: 1 is the earliest

the island at the time of our study. These sites comprised flooded pastures, recently ice-free freshwater wetlands and lagoons near the sea, as well as estuaries and shallow sea bays that ranged from moderate to full salinity. The annual growth of emergent aquatic vascular plants had not yet started, and casual sweep-netting at a water depth of 0–30 cm showed that there was very little invertebrate prey available. We thus surmise that the ducks studied by us fed mainly on remnant last-year seeds and living submerged plants (tubers, perennial leaves, algae). Although we did not quantify food availability, it was obvious that at the very least high-protein aquatic invertebrate prey, often implicated to be very important to dabbling ducks about to nest (Krapu and Reinecke 1992), were very scarce at the time of our study.

Daily mean temperatures were a few degrees above normal during the first 3 days of the sampling period (5–7 °C) and cooler than normal thereafter (1–3 °C) (absolute minimum 0.5 °C, absolute maximum 8 °C). There was precipitation every day (1–20 mm): rain the first 3 days, after that only sleet and snow. The cold spell during the latter half of the study period included persistent gale force winds. The ducks under study thus experienced harsh weather conditions typical or slightly cooler for the area at this time of year.

Time use and behaviour

On each visit at a site we used the 'repeated scan-sampling' to record the behaviour of all visible dabbling ducks (following Altman 1974; Arzel and Elmberg 2004). This was done in a consecutive manner going from one duck to the next, and then starting over again until 20 observations per sex and species had been recorded (compare Altman 1974; Arzel and Elmberg 2004). The final sample obtained at a site on a specific occasion sometimes ended up being less

than 20 behavioural observations because all ducks in a certain category (species and sex) left the area before a full count was obtained or because the maximum daily visit time limit of 60 min for a site had been reached. The risk of recording the same birds at different wetlands during the same day was low due to the short duration of the sampling session per site and the low number of within-sampling session movements of ducks observed flying from one site in the direction of the site to be sampled next. As there is daylight 24 h a day on Andøya in May we sampled behaviour around the clock. At any given site that was sampled more than once we attempted to re-sample at a different time of day than on the previous visit(s).

Following Arzel and Elmberg (2004), Szijj (1965) and Pöysä (1986), we assigned observed behaviours to one of the six following categories: 'interaction' (individuals doing courtship or expressing aggression), 'vigilance', 'comfort' (resting, sleeping and preening individuals), 'movement' (swimming on open water without feeding, walking on land without feeding and spontaneous flight), 'disturbance' (flight due to disturbance) and 'foraging'. Observations pertaining to the latter category we further classified into five different foraging methods: 'foraging on land', 'foraging at the water surface', 'foraging with head under water', 'foraging with head and neck under water' and 'foraging by up-ending'.

The total number of ducks of each sex and species present at a site was also noted.

Analyses

Based on our expectation that time allotment (see preceding text for rationale) to, for example, vigilance and foraging (Paulus 1983; Batt et al. 1992) can be expected to differ between the sexes under specific circumstances, we analysed behavioural data on males and females separately.

We used binomial mixed models to test for behavioural differences between sexes and species and to characterize the relationship between time allocated to different behaviours and the variables body mass, migration distance and nest initiation rank (Table 1). A binomial approach (logistic regression) was used to test the likelihood of an individual being engaged in a given behaviour versus all other behaviours. This likelihood was considered to be representative of the share of time spent doing a behaviour of a certain category. We analysed each behaviour versus all other behaviours in separate models. The six behavioural categories were mutually exclusive, i.e. a bird would be recorded in only one of the categories at a given instance. The number of individuals studied differed among species and sex at a site on any given date. Because some individual birds were repetitively sampled we included the number of individuals per species and sex for which the behaviour was recorded as a random factor when testing for behavioural differences among species and sex. We also included 'site' and 'date' nested within each site as random factors in the models because some sites were sampled on more than one occasion (see "Sample sizes" in the "Results" sections). By nesting the date effect within the site term we thus accounted for between-day differences in weather as well as for possibility that the some individuals may have been observed at more than one sampling occasion.

Models yielding significant differences were subjected to post hoc Tukey test to detect which species differed from which in terms of allocation of time to a certain behaviour. Because the independent variables body mass, migration distance and nest initiation order were all significantly inter-correlated (in males: all $r_s > 0.6$, $p < 0.001$, $n = 90$; in females: $r_s = 0.4, 0.5$ and 0.8 , respectively, $p < 0.002$, $n = 65$), we tested each separately (compare Graham 2003). This means that all data in tables and all tests are based on true counts, whereas the figures illustrate the data as mean proportions in order to facilitate comparison with previous studies.

All statistical analyses were performed in R version 2.15.1 (R Development Core Team 2011). Binomial mixed models were carried out with the `glmer` function in `Lme4` package (Bates et al. 2008). Tukey post hoc tests were performed with the `glht` function in the `multcomp` package (Hothorn et al. 2008, version 1.2-14). Values are presented as mean \pm standard error with significance set at 0.05.

Results

Sample sizes

We obtained a total of 3,053 records of behaviour pertaining to six species of dabbling duck at 21 wetlands

(Table 2). In correlation with the attractiveness of each site to ducks, we visited 13 sites only once, one site twice, six sites three times each and one site five times. In most cases 48+ h lapsed between two visits at any wetland site that was sampled more than once; only one site was sampled twice in <24 h (18 h). Although ducks were observed arriving at and leaving sites, we argue that the probability of sampling the same bird on more than 1 day was small (see "Time use and behaviour"). We do however acknowledge that Mallards which may have been settled early breeders and the few Gadwalls may have been sampled more than once.

Teal was by far the most numerous species, followed by Mallard (Table 2), with individuals of both species seen on all days and at nearly all sites. Observations of Pintail and Wigeon were confined to five and four sites, respectively, while those of Shoveler and Gadwall were scarce, represented by very few individuals. Garganey was not observed during our field work. Due to the global paucity of time use data for spring-staging ducks in the literature we present here the observed proportions of Shoveler and Gadwall (Figs. 2, 3) but did not subject actual count data for these species to statistical testing.

Despite the constant daylight and our efforts to spread observations evenly over each 24-h period, ducks were harder to spot when resting or sleeping in the vegetation during the hours of lowest luminosity (midnight to 3 a.m.), likely leading to a slight under-representation of these behaviours at these hours in the final sample of successful sampling sessions.

Time use per behaviour, sex and species

General patterns

Foraging was the most common time use in all duck species, ranging from 19 % in male Pintail to more than 60 % in female Gadwall (Fig. 2). Comfort behaviours amounted to 20–34 % of activities. Only male Shoveler and female Gadwall used ≤ 11 % of the time for comfort behaviours, but these proportions are based on small samples from few individuals. In all species, interaction and disturbance were marginal behaviours amounting to <7 % of the time. Vigilance time ranged from 8 % in female Mallards to 20 % in male Pintail. Movement amounted to approximately 20 % of the time in most species and sexes.

Differences between sexes in the four common species

Time use patterns generally seemed to differ between sexes in the species with large sample sizes (Fig. 2). Binomial mixed models showed that in three species, Wigeon being the exception, males spent significantly less time foraging

Table 2 Breakdown of sample sizes of dabbling ducks studied at 21 sites on Andøya, Norway, 7–14 May 2008

Species	Days seen (<i>n</i>)	Sites seen (<i>n</i>)	Males (<i>n</i>)			Females (<i>n</i>)		
			Individual ^a	Behaviour records ^b	Foraging records ^c	Individual ^a	Behaviour records ^b	Foraging records ^c
Pintail <i>Anas acuta</i>	7	5	31	198	51	15	117	65
Teal <i>Anas crecca</i>	8	19	117	825	319	78	607	292
Shoveler <i>Anas clypeata</i>	1	1	1	13	5	1	1	
Wigeon <i>Anas penelope</i>	5	4	29	270	106	22	184	71
Mallard <i>Anas platyrhynchos</i>	8	19	98	668	195	24	103	48
Gadwall <i>Anas strepera</i>	2	1	3	49	17	2	18	12

^a Total number of individuals for which behavioural records were obtained, by species and sex

^b Total number of behavioural records

^c The number of behavioural records that could be classified to a certain foraging method

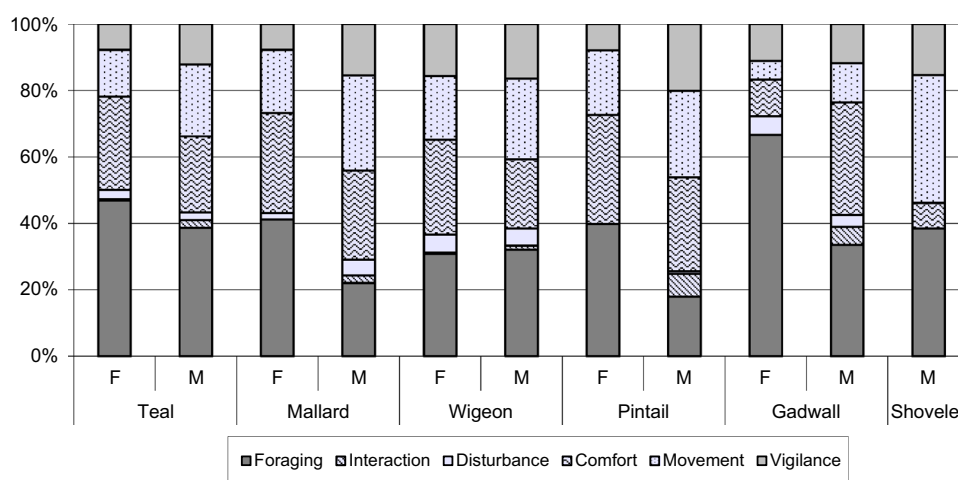


Fig. 2 Relative time use in individual dabbling ducks on Andøya by species and sex (*F* female, *M* male) based on proportions calculated per date and location with occurrence (when >5 behaviours were recorded per sex and species during a sampling session). Classification and definition of the six behavioural categories are given in the

“Time use and behaviour” section. The number of sampled sites and individuals are given in Table 2. Results from Shoveler females were not included because there was only one observation of one individual

and more time vigilant than females (Table 3). Interaction behaviours were more frequently observed in males than in females in Teal only (Table 3); male Teal also spent slightly less time on comfort activities than did females. In terms of ‘gender equality’, the four species thus made up two distinct groups. In Wigeon the sexes did not differ in time use, whereas Mallard, Pintail and, in particular, Teal, males and females exhibited distinctly different time use patterns.

Wigeon females spent significantly less time foraging than the females of the other three species (Fig. 2; Table 4; Appendix 2), but they spend significantly more time in movement than did Pintail and Mallard females. The time spent on interaction, disturbance, comfort, and vigilance did not differ significantly among females of the four species.

Differences among the four common species

Foraging methods

Males of the four common species exhibited similar time budgets in terms of time spent on interaction, disturbance, foraging and comfort (Fig. 2; Table 4; Appendix 1). However, Teal males spent significantly less time vigilant than did Pintail males and less time in movement than did Wigeon males (Table 4; Appendix 1).

General patterns

Foraging methods recorded on Andøya spanned the gradient from terrestrial grazing to up-ending, and when considered as mean proportions varied greatly among species and sometimes between sexes (Fig. 3). Foraging with the neck under water was the most commonly observed foraging method in Teal, Mallard and Pintail, and

Fig. 3 Proportion of foraging time allocated to different foraging methods in dabbling ducks on Andøya per species and sex (*F* female, *M* male), based on proportions calculated per date and location with occurrence (when >5 behaviours were recorded per sex and species during a sampling session). Foraging methods are ordered from the most terrestrial (*bottom*) to the deepest aquatic (*top*). The number of sampled sites and individuals are given in Table 2

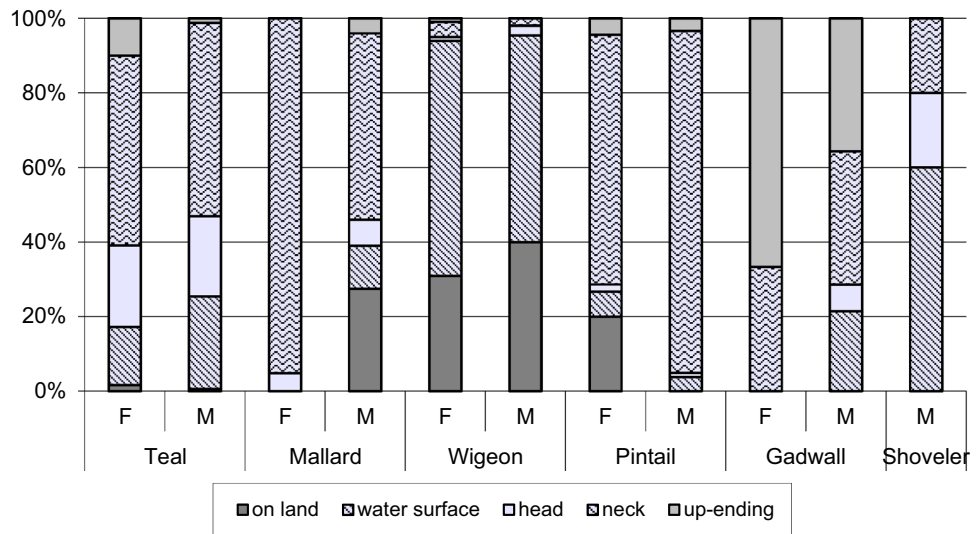


Table 3 Results of species-specific binomial mixed models testing for intersexual differences in allocation of time to six general categories of behaviour in the four common ducks

Species	Number of observations	Behaviour	Estimate ± SE	z	p
Teal <i>Anas crecca</i>	1,432	Interaction	2.025 ± 0.797	2.541	0.011
		Disturbance	-0.008 ± 0.478	-0.016	0.987
		Foraging	-0.357 ± 0.134	-2.677	0.007
		Comfort	-0.346 ± 0.178	-1.95	0.051
		Movement	0.262 ± 0.198	1.318	0.187
		Vigilance	0.737 ± 0.201	3.668	<0.001
Wigeon <i>Anas penelope</i>	454	Interaction	0.783 ± 1.164	0.672	0.501
		Disturbance	-0.096 ± 0.504	-0.191	0.848
		Foraging	-0.138 ± 0.217	-0.636	0.525
		Comfort	-0.445 ± 0.250	-1.778	0.075
		Movement	0.378 ± 0.248	1.522	0.128
		Vigilance	0.246 ± 0.289	0.851	0.395
Pintail <i>Anas acuta</i>	315	Interaction	-2.767 ± 4.256	-0.650	0.516
		Disturbance	N/A		
		Foraging	-1.410 ± 0.314	-4.487	<0.001
		Comfort	0.406 ± 0.462	0.878	0.380
		Movement	-0.217 ± 0.381	-0.569	0.570
		Vigilance	1.608 ± 0.383	4.203	<0.001
Mallard <i>Anas platyrhynchos</i>	771	Interaction	-1.544 ± 1.175	-1.313	0.189
		Disturbance	-0.625 ± 0.742	-0.843	0.399
		Foraging	-1.505 ± 0.328	-4.594	<0.001
		Comfort	0.654 ± 0.351	1.865	0.062
		Movement	0.108 ± 0.332	0.326	0.744
		Vigilance	1.280 ± 0.438	2.923	0.003

Each behaviour was tested in a separate model (see “Analyses”). Site and date nested within site were used as random factors. Significant test outcomes are given in boldface and mean that males differ from females. A positive estimate indicates a relative higher number of males displaying a behaviour than females

SE, Standard error; N/A, test not applicable due to small sample size

Observations on Shoveler *Anas clypeata* and Gadwall *Anas strepera* were scarce, represented by very few individuals, and therefore not subjected to detailed analysis

Table 4 Comparison of the number of observations allocated to six classes of behaviour versus all other behaviours for males and females in the four common species of ducks at late-spring staging sites on Andøya

Males/females	Number of observations	Pintail	Teal	Wigeon	Mallard
Males					
Interaction	33	-4.81 ± 0.78 a	-4.79 ± 0.56 a	-4.87 ± 0.90 a	-5.72 ± 0.69 a
Disturbance	52	-5.35 ± 0.71 a	-4.90 ± 0.51 a	-5.07 ± 0.58 a	-4.75 ± 0.50 a
Foraging	671	-0.92 ± 0.38 a	-0.79 ± 0.32 a	-1.19 ± 0.37 a	-1.21 ± 0.33 a
Comfort	508	-2.30 ± 0.57 a	-1.91 ± 0.54 a	-2.04 ± 0.58 a	-1.69 ± 0.54 a
Movement	395	-1.28 ± 0.28 a, b	-1.34 ± 0.19 a	-0.73 ± 0.26 b	-1.22 ± 0.20 a, b
Vigilance	302	-1.27 ± 0.21 a	-2.09 ± 0.16 b	-1.51 ± 0.24 a, b	-1.72 ± 0.15 a, b
Females					
Interaction	6	-6.40 ± 1.50 a	-7.14 ± 1.20 a	-5.36 ± 1.55 a	-4.53 ± 1.06 a
Disturbance	22	N/A	-5.71 ± 0.74 a	-5.74 ± 0.82 a	-4.54 ± 0.89 a
Foraging	476	-0.23 ± 0.78 a	-0.64 ± 0.63 a	-2.17 ± 0.70 b	-0.34 ± 0.73 a
Comfort	272	-1.07 ± 0.62 a	-1.49 ± 0.46 a	-0.68 ± 0.56 a	-1.63 ± 0.59 a
Movement	155	-2.84 ± 0.56 a	-2.11 ± 0.42 a, b	-1.08 ± 0.51 b	-2.71 ± 0.55 a
Vigilance	80	-2.73 ± 0.44 a	-2.70 ± 0.25 a	-2.04 ± 0.35 a	-2.75 ± 0.48 a

Each behaviour was tested in a separate model (see “Analyses”). Parameter estimate (\pm SE) of the binomial mixed models testing for interspecific differences in allocation of time are presented. Values followed by different lowercase letters indicate significant differences at $p < 0.05$ according to GLMM binomial and Tukey's post hoc tests

foraging at the water surface was the second-most adopted method within the guild. Terrestrial feeding was a common foraging method in Wigeon females and males, Mallard males and Pintail females, but this foraging method was rare to non-existent in all other species. Up-ending was rare in all species except Gadwall, in which females especially stand out as ‘extreme deep foragers’. Gadwall also stands out as a species with a large difference in foraging method between the sexes. However, the patterns observed in both Gadwall and Shoveler are based on data from very few individuals (Table 2).

Differences between sexes within the four common species

There was no significant difference between Wigeon and Pintail males and females in terms of allocation of time to different foraging behaviours (Table 5). However, Teal and Mallard males engaged significantly less in the riskier foraging methods and more in those allowing vigilance (Table 5). Teal males foraged more at the water surface and did less up-ending than Teal females. Mallard females allocated more time to foraging with the neck under water than did Mallard males.

Differences among the four common species

In terms of males foraging on land, high variance and limited sample sizes contributed to no significant differences being found between the species (compare Fig. 3 with Table 6; Appendix 3). However, Wigeon males foraged significantly

more at the water surface and less with the neck under water than did those of Teal, Mallard and Pintail. No male Wigeon was observed foraging by up-ending. Wigeon males thus used less risky behaviours by foraging at the water surface and on land while the three deeper foraging methods accounted for more than half of the foraging time in Teal, Mallard and Pintail males. Pintail males foraged significantly more in deep water than those of Mallard and Wigeon; Teal and Mallard males were more generalist and opportunist foragers, utilizing the entire depth gradient.

In females, Wigeon stands out as foraging essentially on land and significantly more so than all other three species (Fig. 3; Table 6; Appendix 4). No female Mallard was observed foraging on land. Wigeon females also foraged more at the water surface than Teal females and less with the neck under water than all of the other species.

Time use in relation to body mass, migration distance and nest initiation order

A significant relationship between body mass and time allocated to a behavioural category was observed in males only; heavier species allocated less time to foraging but more to vigilance than smaller ones (Table 7). In those species migrating shorter distances, females were more sensitive to disturbance, while males spent more time on comfort activities (Table 7). Finally, timing of nest initiation was related to certain behavioural categories in females only; early breeders foraged more and displayed less movement (Table 7).

Table 5 Result of species-specific binomial mixed models testing for intersexual differences in allocation of time to five categories of foraging method in the four common ducks

Species	Number of observations	Foraging method	Estimate ± SE	z	p
Teal <i>Anas crecca</i>	611	On land	0.074 ± 1.196	0.062	0.951
		Water surface	0.5 ± 0.252	1.983	0.047
		Head under water	0.155 ± 0.242	0.641	0.522
		Neck under water	-0.374 ± 0.228	-1.645	0.100
		Up-ending	-3.069 ± 1.327	-2.313	0.021
Wigeon <i>Anas penelope</i>	177	On land	-0.364 ± 0.355	-1.024	0.306
		Water surface	0.329 ± 0.347	0.949	0.343
		Head under water	1.286 ± 1.164	1.105	0.269
		Neck under water	-0.491 ± 0.810	-0.606	0.544
		Up-ending	N/A		
Pintail <i>Anas acuta</i>	116	On land	-5.357 ± 3.803	-1.409	0.159
		Water surface	-5.358 ± 4.174	-1.284	0.199
		Head under water	-0.462 ± 1.239	-0.373	0.709
		Neck under water	0.119 ± 0.711	0.167	0.867
		Up-ending	0.499 ± 0.939	0.531	0.595
Mallard <i>Anas platyrhynchos</i>	243	On land	N/A		
		Water surface	1.988 ± 1.256	1.583	0.113
		Head under water	1.830 ± 0.715	1.162	0.245
		Neck under water	-1.726 ± 0.651	-2.651	0.008
		Up-ending	3.199 ± 3.583	0.893	0.372

Site and date nested within site were used as random factors. Significant test outcomes are given in boldface and mean that males differ from females. A positive estimate indicates a relative higher number of males displaying a behaviour than females

Table 6 Comparison of the number of observations allocated to five categories of foraging method versus all other foraging methods for males and females in four species of ducks at late-spring staging sites on Andøya

Males/females	Number of observations	Pintail	Teal	Wigeon	Mallard
Males					
On land	97	-19.45 ± 6.08 a	-22.50 ± 5.98 a	-8.79 ± 5.12 a	-9.63 ± 5.19 a
Water surface	176	-3.54 ± 1.15 a	-1.27 ± 0.64 a	1.24 ± 0.78 b	-1.89 ± 0.69 a
Head under water	85	-4.77 ± 1.14 a	-2.19 ± 0.36 a	-2.81 ± 0.67 a	-1.98 ± 0.40 a
Neck under water	296	1.94 ± 1.14 a	0.02 ± 0.88 a,c	-6.19 ± 1.24 b	-1.38 ± 0.91 c
Up-ending	17	-9.19 ± 3.83 a	-9.98 ± 3.13 a	N/A	-10.54 ± 3.23 a
Females					
On land	36	-5.09 ± 1.47 a	-7.66 ± 1.64 a	0.70 ± 1.79 b	N/A
Water surface	89	-3.03 ± 1.29 a, b	-2.50 ± 0.83 a	-0.47 ± 0.98 b	-2.73 ± 1.32 a, b
Head under water	65	-2.60 ± 0.96 a	-1.62 ± 0.49 a	-4.33 ± 1.20 a	-1.48 ± 0.83 a
Neck under water	268	0.18 ± 1.09 a	0.09 ± 0.86 a	-4.85 ± 1.28 b	-0.06 ± 1.10 a
Up-ending	18	-7.26 ± 2.34 a	-7.14 ± 1.70 a	-7.26 ± 2.04 a	-4.37 ± 2.37 a

Each foraging method was tested in a separate model (see “Analyses”). Parameter estimate (±SE) of the binomial mixed models testing for interspecific differences in time allocated to each foraging method are presented. Values followed by different lowercase letters indicate significant differences at $p < 0.05$ according to GLMM binomial and Tukey’s post hoc tests

Discussion

Time use

General patterns and interspecific differences

The most common class of behaviour in pre-breeding dabbling ducks on Andøya was that of foraging behaviours.

As this study is the first to examine time use in newly arrived dabbling ducks at such a northerly location, we could only compare our data with data on similar populations arriving at more southern sites in the general migratory flyway. Based on data from a study in Sweden, dabbling ducks on Andøya spent rather less time foraging than did their more southerly spring-staging congeners (compare Fig. 1 in Arzel et al. 2007). In the latter study

Table 7 Result of binomial mixed models testing the relation between time use (column 'behaviour') and body mass, migration distance and nest initiation order

Independent variable	Sex	Behaviour	Slope ± SE	z	p		
Body mass	Female	Interaction	0.003 ± 0.002	1.632	0.103		
		Disturbance	6e-4 ± 0.001	0.431	0.666		
		Foraging	7e-04 ± 5e-04	-1.201	0.230		
		Comfort	6e-04 ± 6e-04	0.959	0.338		
		Movement	-3e-4 ± 5e-4	-0.550	0.582		
		Vigilance	5e-04 ± 6e-04	0.738	0.460		
	Male	Interaction	-0.001 ± 7e-04	-1.359	0.174		
		Disturbance	6e-5 ± 5e-4	0.115	0.909		
		Foraging	-0.001 ± 2e-04	-2.156	0.031		
		Comfort	1e-04 ± 2e-04	0.656	0.512		
		Movement	1e-4 ± 2e-4	0.719	0.472		
		Vigilance	6e-04 ± 2e-04	2.896	0.004		
		Migration distance	Female	Interaction	-9e-04 ± 9e-04	-0.972	0.331
				Disturbance	-0.001 ± 6e-04	-2.470	0.014
Foraging	-3e-04 ± 2e-04			-1.524	0.127		
Comfort	4e-04 ± 2e-04			1.822	0.068		
Male	Movement		4e-5 ± 2e-4	0.199	0.842		
	Vigilance		1e-04 ± 3e-04	0.454	0.650		
	Interaction		5e-04 ± 3e-04	1.448	0.148		
	Disturbance		-3e-04 ± 3e-04	-1.038	0.299		
Nest initiation order	Female	Foraging	1e-04 ± 1e-04	1.109	0.267		
		Comfort	-3e-04 ± 1e-04	-2.504	0.012		
		Movement	7e-5 ± 1e-4	0.593	0.553		
		Vigilance	1e-04 ± 1e-04	1.303	0.192		
		Interaction	-0.703 ± 0.517	-1.361	0.174		
	Male	Disturbance	-0.401 ± 0.360	-1.117	0.264		
		Foraging	-0.495 ± 0.166	-2.988	0.003		
		Comfort	0.232 ± 0.164	1.413	0.158		
		Movement	0.460 ± 0.170	2.710	0.007		
		Vigilance	0.241 ± 0.186	1.296	0.195		
Male	Interaction	0.366 ± 0.246	1.485	0.137			
	Disturbance	-0.077 ± 0.141	-0.543	0.587			
	Foraging	0.077 ± 0.073	1.054	0.292			
	Comfort	-0.110 ± 0.080	-1.385	0.166			
	Movement	0.068 ± 0.064	1.064	0.288			
		Vigilance	-0.083 ± 0.070	-1.183	0.237		

Body mass and migration distance are given as actual means, while nest initiation order data are ranks. Site and date nested within site were both used as random factors. Females and males were analysed separately. All four species differ in body mass and in distance travelled. Behavioural categories are defined in the "Analyses" section. Significant relationships are shown in boldface. Results are based on 1,011 observations for females and 1,961 observations for males

dabbling ducks spent relatively more time foraging during migration compared to when migration was more or less over and nesting became more imminent, suggesting that the energetic stress is higher during migration than in the anticipation of nesting. In general, our results support this observation. Further comparison with studies carried out in the spring at more southern sites in Fennoscandia is more difficult as they were not based on 24-hour time use data.

Extending the comparison to other parts of the annual cycle, Guillemain et al. (2002) found that Teal males and females studied during the entire 'winter' (September–March) used 10–40 % of the diurnal time (07:00–18:00

and 85–95 % of the nocturnal time for foraging. These authors also observed Mallard, reporting that males and females of this species spent 5–20 % of the day and 70–90 % of the night foraging. In our study and using the same time interval (07:00–18:00 h) Teal females and males spent 45 and 35 % of the time foraging, respectively, while Mallard females and males spent 61.5 and 28 % of the time foraging, respectively. Time allocated to foraging during the 'nocturnal' time interval (compare Guillemain et al. 2002) was much less in our study: 58 and 44 % of Teal females and males, respectively, and 37 and 34 % of Mallard females and males, respectively. Cautiously

combining these figures with those reported by Arzel et al. (2007) suggests that for Teal males and females, the daily proportion spent foraging is high throughout the winter, peaks during spring migration and remains high in pre-breeding birds. In this context, the foraging activity of Teal on Andøya is the lowest recorded, which is contrary to the prediction that this long-distance migrant arrives at sub-arctic Norway in an energetically depleted state.

Intersexual differences

As clearly shown in Table 3, three of the four species observed on Andøya for which we had an adequate sample showed a significant intersexual difference in terms of the time used for vigilance and foraging (also for Teal interaction). This result implies that the 'sex roles' are more pronounced on Andøya than at the 'half-way' staging site in southern Sweden, where the same species were studied but only Mallard showed any significant behavioural difference between males and females (Arzel and Elmberg 2004). The results of our study thus support the predictions that as ducks get nearer to the breeding grounds, females allocate more time to foraging (compare Paquette and Ankney 1998) and males spend relatively more time looking for predators and competing males.

Of the four common species on Andøya, Teal exhibited an intersexual difference in time use in the highest number of behavioural categories (Table 3; Fig. 2). We argue that this is not only due to the higher power in the statistical test due to the larger sample size in this species, but that there may be also biologically relevant reasons underlying the result. Teal is the most abundant species and often occurs in larger flocks than the other species; consequently, it is likely that Teal males need to guard their females more frequently against other males than do males of these other species. This need could explain the higher number of intraspecific interactions recorded among Teal males compared to those among Teal females.

Foraging methods

General patterns and interspecific differences

Dabbling ducks are often seen as a textbook example of a guild in which interspecific differences in microhabitat use and foraging method lead to niche segregation, precluding competition and thus allowing co-occurrence of more species (Nudds et al. 2000; compare Lack 1947). Indeed, the general impression from the foraging method data as shown in Fig. 3 supports a pattern prevalent in earlier studies of the community ecology of dabbling ducks, namely that even though all species may use all foraging methods from time to time, the four common species on

Andøya can be characterized as follows: Mallard and Teal are generalists, feeding at all depths and hence using all parts of the habitat gradient; Wigeon is the 'terrestrial grazer' compared to the other species; the long-necked Pintail is the 'deep water specialist'. The only other study carried out in the spring which we can use as a comparison is that of Arzel and Elmberg (2004), whose site was some 1,500 km farther south than Andøya but who used a microhabitat classification rather than one based on foraging method. The 'roles' of the species and their 'foraging niche specialization' seem to be identical in these two studies. However, the degree to which dabbling ducks actually compete for food, both spatially and temporally, remains an open question (Gunnarsson et al. 2013). A word of caution is warranted, as is evident from Table 6 and Appendices 3 and 4, there is a wide interspecific overlap in foraging method, even when the sexes are considered separately. Statistically speaking, in terms of foraging method, Wigeon is significantly different from all other species, Pintail is significantly different from Mallard, but Mallard and Teal do not significantly differ in any foraging behaviour in either sex. In contrast, Johnson and Rohwer (2000) found that the Green-winged Teal foraged in significantly shallower habitats than Mallards. However, the former is a different species than Teal and the study was carried out on tidal mudflats during the winter. Within a paradigm of competition and niche segregation it may seem odd that Teal and Mallard have such similar proportions of deeper foraging methods, but their different neck length, depth reach and bill lamellar density lead to quite different de facto feeding niches in these two species even if the recorded behavioural patterns are very similar (compare Nudds et al. 2000).

Intersexual differences

Our results on foraging method should be interpreted bearing in mind that it may not be independent within pairs, as males stay close to females for mate guarding and vigilance. This may restrict the possibility of paired males choose their foraging depth and thus utilize specific foraging methods. For example, we found that Teal, Pintail and Mallard males allocate more time to vigilance than do the females of these species. Given this temporal restriction, Teal and Mallard males on Andøya foraged in significantly shallower water than females. By foraging closer to the water surface they are more likely to detect and respond to a threat (predation or other males) and thus guard their mates more efficiently. Paired females are thus permitted to forage at the depth where food resources are the most profitable to them in terms of intake rate. Note, however, that males did not consistently use foraging methods that would also enable maintenance of greatest

vigilance (such as terrestrial feeding and bill-dipping), indicating that they too must engage in some riskier foraging in order to meet their energy demands. In a previous flyway-level study of Teal, Guillemain et al. (2007a) showed that both sexes adopt gradually deeper (and thus riskier) foraging methods as they progress farther north in the flyway, in response to lower predation risk. It is a priority for future research to determine the extent of the dependency of this response on the pairing status of birds—in other words, to assess ‘the cost of being paired’ in males and ‘the benefit of being paired’ in females (compare Guillemain et al. 2007b).

Time use in relation to body mass, migration distance and nest initiation order

The theory of income versus capital breeding strategies (Jönsson 1997) predicts that, given their relatively low body mass, most dabbling ducks should be income breeders (Meijer and Drent 1999; Klaassen 2002). This is especially true for the smallest species (for example, Green-winged Teal in Paquette and Ankney 1998), whereas larger-bodied species may rely at least in part on endogenous stores (for example, Pintail; Esler and Grand 1994; Baldassarre and Bolen 2006). If so, species with a larger body mass should have less depleted energy stores after migration and hence need to spend less time foraging than those with a lower body mass (Klaassen 2002). On this basis, we would predict for the Andøya guild that foraging time should increase in the order: Mallard < Pintail < Gadwall < Wigeon < Shoveler < Teal (see Table 1 for body mass values). Data from males on Andøya support this prediction (Fig. 2; Table 7): the heavier species foraged less and could thus allocate more time to other behaviours, such as vigilance. Females, on the other hand, did not meet this prediction.

The hypothesis that species having a shorter migration distance should have less depleted energy stores (Dugger and Petrie 2000) leads to the prediction that time spent foraging should increase among the dabbling ducks observed on Andøya in the order Mallard < Teal < Gadwall < Wigeon < Shoveler < Pintail (cf. Table 1). However, our data did not support this hypothesis (Fig. 2; Tables 4, 7). Males of species migrating shorter distances spent rather more time in recuperating activities than did those of species migrating longer distances, suggesting that they have more stored nutrients. Nevertheless, females migrating shorter distances spent more time in disturbance flight than did their longer distance counterparts, which may be a consequence of less depleted energy stores in the former allowing them to take less risk, such as when raptors appear. It should be noted that these conclusions are based on general recovery patterns (e.g. Gjershaug et al.

1994; Wernham et al. 2002), while the actual distances travelled by the birds studied at Andøya remain unknown.

The hypothesis that species nesting early should spend more time foraging than late nesters rests on the notion that the former have to deal with recuperation from migration and breeding costs at the same time. Accordingly, time spent foraging should increase in the order Wigeon/Gadwall/Shoveler < Teal < Pintail < Mallard in the guild studied here (see Table 1). Data from the four common species on Andøya provide support for this hypothesis for females only (Table 7); early breeders foraged more and moved less than later breeders.

Behavioural data from pre-breeding long-distance migrating ducks on Andøya thus partly lend support to all three hypotheses on foraging intensity addressed above. In general, dabbling ducks on Andøya spent surprisingly little time foraging considering that most of them had just finished a very long migratory journey. Rather, they appeared to arrive on Andøya, northern Norway, in a condition that did not require intensive feeding to recuperate. Our data on foraging method conform very well to data from previous studies by indicating a moderate de facto niche segregation among the species in the dabbling duck guild.

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Appendix 1

Pairwise post-hoc Tukey tests of interspecific differences in the number of observations allocated to six categories of behaviour in males of Mallard, Teal, Wigeon, and Pintail

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
Interaction	Teal	Pintail	0.022	1
	Wigeon	Pintail	−0.059	1
	Mallard	Pintail	−1.169	0.636
	Wigeon	Teal	−0.088	1
	Mallard	Teal	−1.512	0.418
	Mallard	Wigeon	−0.907	0.794

continued

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
Disturbance	Teal	Pintail	0.761	0.868
	Wigeon	Pintail	0.425	0.973
	Mallard	Pintail	0.961	0.766
	Wigeon	Teal	-0.381	0.981
	Mallard	Teal	0.364	0.983
	Mallard	Wigeon	0.715	0.888
Foraging	Teal	Pintail	0.519	0.953
	Wigeon	Pintail	-0.869	0.816
	Mallard	Pintail	-1.083	0.692
	Wigeon	Teal	-1.659	0.337
	Mallard	Teal	-2.213	0.115
	Mallard	Wigeon	-0.071	1
Comfort	Teal	Pintail	1.518	0.417
	Wigeon	Pintail	0.749	0.873
	Mallard	Pintail	2.399	0.074
	Wigeon	Teal	-0.473	0.964
	Mallard	Teal	1.081	0.693
	Mallard	Wigeon	1.231	0.598
Movement	Teal	Pintail	-0.270	0.993
	Wigeon	Pintail	1.810	0.260
	Mallard	Pintail	0.218	0.996
	Wigeon	Teal	2.596	0.045
	Mallard	Teal	0.709	0.890
	Mallard	Wigeon	-2.127	0.138
Vigilance	Teal	Pintail	-3.927	<0.001
	Wigeon	Pintail	-0.842	0.829
	Mallard	Pintail	-2.068	0.158
	Wigeon	Teal	2.240	0.108
	Mallard	Teal	2.139	0.135
	Mallard	Wigeon	-0.888	0.805

Significant relationships are shown in boldface. Results are based on 1,961 observations

Appendix 2

Pairwise post-hoc Tukey tests of interspecific differences in the number of observations allocated to six categories of behaviour in females of Mallard, Teal, Wigeon, and Pintail

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
Interaction	Teal	Pintail	-0.550	0.944
	Wigeon	Pintail	0.498	0.958
	Mallard	Pintail	1.166	0.639
	Wigeon	Teal	0.942	0.775
	Mallard	Teal	1.908	0.217
	Mallard	Wigeon	0.501	0.957

continued

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
Disturbance	Teal	Pintail	0	1
	Wigeon	Pintail	0	1
	Mallard	Pintail	0	1
	Wigeon	Teal	-0.034	1
	Mallard	Teal	1.376	0.459
	Mallard	Wigeon	1.361	0.469
Foraging	Teal	Pintail	-0.956	0.760
	Wigeon	Pintail	-3.098	0.010
	Mallard	Pintail	-0.246	0.994
	Wigeon	Teal	-3.676	0.001
	Mallard	Teal	0.724	0.879
	Mallard	Wigeon	3.373	0.004
Comfort	Teal	Pintail	-1.005	0.735
	Wigeon	Pintail	0.639	0.915
	Mallard	Pintail	-1.134	0.656
	Wigeon	Teal	1.834	0.246
	Mallard	Teal	-0.342	0.985
	Mallard	Wigeon	-1.725	0.298
Movement	Teal	Pintail	1.835	0.247
	Wigeon	Pintail	3.039	0.012
	Mallard	Pintail	0.270	0.993
	Wigeon	Teal	2.370	0.079
	Mallard	Teal	-1.443	0.460
	Mallard	Wigeon	-2.979	0.015
Vigilance	Teal	Pintail	0.078	1
	Wigeon	Pintail	1.327	0.536
	Mallard	Pintail	-0.020	1
	Wigeon	Teal	1.835	0.249
	Mallard	Teal	-0.092	1
	Mallard	Wigeon	-1.284	0.563

Significant relationships are shown in boldface. Results are based on 1,011 observations

Appendix 3

Post-hoc Tukey tests of interspecific differences in the number of observations allocated to different foraging methods (column 'behaviour') in Teal, Wigeon, Mallard and Pintail males

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
On land	Teal	Pintail	-1.168	0.601
	Wigeon	Pintail	1.826	0.221
	Mallard	Pintail	1.690	0.284
	Wigeon	Teal	2.448	0.054
	Mallard	Teal	2.222	0.095
	Mallard	Wigeon	-0.474	0.957

continued

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
Water surface	Teal	Pintail	2.328	0.084
	Wigeon	Pintail	4.548	<0.001
	Mallard	Pintail	1.441	0.453
	Wigeon	Teal	4.166	<0.001
	Mallard	Teal	-1.098	0.673
Head under water	Mallard	Wigeon	-4.630	<0.001
	Teal	Pintail	2.323	0.083
	Wigeon	Pintail	1.551	0.382
	Mallard	Pintail	2.382	0.072
	Wigeon	Teal	-0.926	0.775
Neck under water	Mallard	Teal	0.479	0.960
	Mallard	Wigeon	1.228	0.585
	Teal	Pintail	-2.415	0.069
	Wigeon	Pintail	-6.833	<0.001
	Mallard	Pintail	-3.623	0.002
Up-ending	Wigeon	Teal	-6.385	<0.001
	Mallard	Teal	-2.306	0.091
	Mallard	Wigeon	4.763	<0.001
	Teal	Pintail	-0.311	0.987
	Wigeon	Pintail	0.000	1.000
Up-ending	Mallard	Pintail	-0.431	0.967
	Wigeon	Teal	0.000	1.000
	Mallard	Teal	-0.243	0.994
	Mallard	Wigeon	0.000	1.000

Behavioural categories are defined in the “Analyses” section. Significant relationships are shown in boldface. Results are based on 671 observations

Appendix 4

Post-hoc Tukey tests of interspecific differences in the number of observations allocated to different foraging methods (column ‘behaviour’) in Teal, Wigeon, Mallard and Pintail females

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
On land	Teal	Pintail	-2.299	0.073
	Wigeon	Pintail	2.910	0.013
	Mallard	Pintail	N/A	
	Wigeon	Teal	3.924	<0.001
	Mallard	Teal	N/A	
Water surface	Mallard	Wigeon	N/A	
	Teal	Pintail	0.513	0.953
	Wigeon	Pintail	2.135	0.132
	Mallard	Pintail	0.215	0.996
	Wigeon	Teal	3.145	0.008
Water surface	Mallard	Teal	-0.197	0.997
	Mallard	Wigeon	-1.750	0.280

continued

Behaviour	Species 1	Species 2	<i>z</i>	<i>p</i>
Head under water	Teal	Pintail	1.090	0.680
	Wigeon	Pintail	-1.201	0.609
	Mallard	Pintail	1.208	0.604
	Wigeon	Teal	-2.386	0.074
	Mallard	Teal	-0.179	0.998
Neck under water	Mallard	Wigeon	2.085	0.147
	Teal	Pintail	-0.132	0.999
	Wigeon	Pintail	-4.018	<0.001
	Mallard	Pintail	-0.266	0.993
	Wigeon	Teal	-4.926	<0.001
Up-ending	Mallard	Teal	-0.154	0.999
	Mallard	Wigeon	3.541	0.002
	Teal	Pintail	0.065	1
	Wigeon	Pintail	0.003	1
	Mallard	Pintail	1.280	0.663
Up-ending	Wigeon	Teal	-0.066	1
	Mallard	Teal	1.046	0.703
	Mallard	Wigeon	1.103	0.668

Behavioural categories are defined in the “Analyses” section. Significant relationships are shown in boldface. Results are based on 471 observations

N/A, Test not applicable due to small sample size

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