

Interspecific variation in time budgets among sympatric dabbling ducks

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Abstract

The effect of some of the ecological differences among Swedish dabbling ducks, population densities and sex ratios on the proportion of time allocated to foraging was studied during the breeding season 1986 and 1987. Time budget data were collected at southern Gotland, Sweden, and correlation analyses were done with ecological differences determined from the literature and from observations. Increasing male bias in the sex ratios increased the amount of time spent vigilant early in the breeding season for both sexes in April 1987 and for males in May 1987, and also increased the amount of movements of males in April 1987 and of females in May 1986, but decreased movements of males in June 1986. The amount of time spent vigilant did also decrease with increasing male bias for females in June 1986. The proportion of time spent foraging by females in May 1986, but also in May 1987 and June 1986, decreased as the male bias increased. In

early breeding season (April), the proportion of time devoted to aggressions (for males) and movements (for females) were positively correlated with the population densities. This did not, however, lead to decreased foraging time. In late season (July) the foraging time was positively correlated with population densities, indicating intraspecific exploitative competition for prey. Migration distance and degree of carnivory did not influence amount of time allocated to foraging. In conclusion, it was shown that sex ratios and population densities did influence time allocation among dabbling ducks during some parts of the breeding season.

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Introduction

Among seasonally reproducing animals time and energy allocation during the breeding season can be expected to greatly influence reproductive success (King 1974). The proportion of time devoted to e.g. foraging can thus be expected to reflect the needs and the restrictions that an animal is experiencing in a given situation.

The need of foraging generally increases with energy demanding processes such as reproduction and migration. In some situations, however, there can be a time lag between gathering the energy and using it (Krapu 1981). Use of energy reserves thus can influence time allocation (Thompson & Raveling 1987). Moreover, both food quantity and quality may influence total foraging time (Sih 1984, Stephens & Krebs 1986).

Behavioural demands can to some extent restrict the time available to foraging, e.g. avoiding predators and

behaviours associated with reproduction are assumed to interfere with foraging (Sih 1980, Lima 1985, Clark & Ricklefs 1988). Under intraspecific interference competition, large population densities and/or biased sex ratios may increase the demands for other activities than foraging, such as vigilance and aggressions (Mjelstad & Saetersdal 1988).

Much of this is well documented, especially among birds (e.g. Brown & Fredrickson 1987, Austin 1987, Masman et al. 1988, Mace 1989), but only a few studies have had the opportunity to make comparisons using species with different demands and restrictions but still experiencing approximately the same environmental conditions (e.g. Bergan et al. 1989). A group of similar species breeding in the same habitat can provide this opportunity.

The dabbling ducks (Anatidae) form a guild of species that show large ecological similarities. Still, there are differences in e.g. migration distances (Perdeck & Clason 1981, Pettersson et al. 1986), degree of territoriality (Nudds & Ankney 1982), habitat use (Nudds 1983), diet choice (Swanson & Duebbert 1989), prey size choice (Nudds & Bowlby 1984) and nest site selection (Bengtson 1970, Swanson & Duebbert 1989).

Some of the ecological differences between the species of dabbling ducks can be expected to influence the proportion of time allocated to foraging. The following predictions can be made. Large migration distances can be expected to increase the amount of time spent foraging in early and late breeding season. Because energy and nutrients are thought to be limiting resources during breeding and moulting (Bluhm 1988), larger degree of carnivory would decrease the time needed to fulfil the nutritional requirements of the ducks and thus also decrease the amount of time needed for foraging (Paulus 1988). Intraspecific exploitative competition would probably force the individuals to spend more time foraging at high population densities because of suppressed prey densities. On the other hand, when there is intraspecific interference competition, larger population densities would decrease time available for foraging as encounter rate between conspecifics increase (Mjelstad & Saetersdal 1988). A male biased functional sex ratio can also be expected to increase the interference competition which should increase the proportion of time allocated to vigilance, aggressions and locomotion and thus decrease time available to foraging.

To determine how such ecological differences can influence foraging time allocation I have established time budgets for seven dabbling duck species residing in the same habitat during the breeding season.

Methods

Time budget data were collected at southern Gotland, Sweden (57°00' N, 18°20' E) in 1986 and 1987. All seven dabbling duck species breeding in Sweden are known to occur regularly in this area during the breeding season. They are Mallard *Anas platyrhynchos*, Pintail *Anas acuta*, Gadwall *Anas strepera*, Shoveler *Anas clypeata*, Garganey *Anas querquedula*, Teal *Anas crecca* and Wigeon *Anas penelope*. The study area consisted of the shallow, eutrophic lake Stockviken, the nearby sea and the land area in between. Lake Stockviken is approximately 50 ha in size and most of the shore is surrounded by *Phragmites australis*. The surroundings of the lake mainly consists of pastures and some farmland. The area between the lake and the sea shore is extensively grazed by cattle and sheep. The

Table 1. The two variables used for classification of the dabbling ducks, obtained from literature data.

De två variabler som användes för klassificering av simänderna, hämtat från litteraturredata.

Species	Migration distance ^a km+SD(n)	Degree of carnivory ^b
Art	Flyttnings- avstånd	Grad av animaliediet
Mallard <i>Gräsand</i>	745±407 (641)	2
Pintail <i>Stjärtand</i>	1321±462 (24)	2
Gadwall <i>Snatterand</i>	1378±410 (9)	1
Shoveler <i>Skedand</i>	1667±486 (11)	4
Garganey <i>Årta</i>	2589±2184 (3)	3
Teal <i>Kricka</i>	1395±346 (196)	2
Wigeon <i>Bläsand</i>	1188±390 (14)	1

^aMean distance in km from ringing station at Öland to winter recoveries and controls.

Medelavstånd i km från ringmärkningsstationen på Öland till kontroller och återfynd vintertid.

^bSummer diet determined from the literature (see references in the text). High values indicate high proportion of animals in summer diet.

Diet under sommaren uppskattad från litteraturuppgifter (för referencer se texten). Höga värden indikerar hög andel animalier i dieten sommartid.

shore is shallow and stony. From an observation tower at the shore of the lake the whole area was observed using a spotting scope (20-60×).

The ecological differences between the dabbling ducks regarding migration distance and degree of carnivory were determined from the literature (see Table 1). Mean migration distances in km from the ringing station at Ottenby at southern Öland (approximately 140 km southwest of the study area) to the sites of winter recoveries and controls were measured and calculated from the maps in Petterson et al. (1986). Degree of carnivory was determined from summer diets mainly from Swanson & Duebbert (1989), with additional information on Green-winged Teal *Anas crecca* and Wigeon *Anas penelope* or *Anas americana*, (see below) from Spärck (1947), Olney (1965), Cramp & Simmons (1977), Bartonek (1972) and Danell & Sjöberg (1980). In the classification regarding degree of carnivory I have assumed that American Wigeon *Anas americana* and Blue Winged Teal *Anas discors* are ecologically equivalent to European Wigeon *Anas penelope* and Garganey *Anas querquedula*, respectively. The relative population densities and proportions of males of each species each year and month were calculated using the time budget data (see Table 2 and Table 3).

Table 2. Observed relative population densities of the dabbling ducks. Expressed as mean number of individuals observed per scan of each species, calculated as total number of notations of each species divided by the total number of scans.

Observerade relativa populationstätheter hos simänderna. Uttryckt som medelantalet individer observerat per kikarsvep av varje art, uträknat som totalt antal noteringar av varje art delat med antalet kikarsvep.

Species Art	1986			1987			
	May	June	July	April	May	June	July
Mallard <i>Gräsand</i>	2.1	10.0	9.6	6.2	9.0	9.2	7.7
Pintail <i>Stjärtand</i>	0.7	1.6	1.2	1.2	2.1	2.1	1.2
Gadwall <i>Snattherand</i>	0.5	1.6	0.2	1.0	1.5	2.7	0.2
Shoveler <i>Skedand</i>	4.8	12.9	4.8	9.9	10.3	5.0	1.9
Garganey <i>Årta</i>	1.3	0.2	0.5	0.0	1.4	0.6	0.02
Teal <i>Kricka</i>	1.5	4.9	3.3	5.9	0.3	1.8	0.3
Wigeon <i>Bläsand</i>	0.3	1.2	0.04	3.7	1.5	1.5	0.05

During 1986 time budget data were collected in May, June and July, in 1987 in April, May, June and July by instantaneous scan sampling (Altman 1974). The behaviours of all observable dabbling ducks in the area were scanned at a constant interval during a scanning period. An interval as short as possible (3-20 minutes) was used between each scan. Most scanning periods lasted for two hours, but occasionally the observations were interrupted and thus some periods were shorter. The scanning periods were evenly spread over the light part of the day. The observed ducks were separated by species, age and sex when possible. Only observations of adult ducks were included in April, May and June. In July it was not possible to surely separate fully grown ducklings from adults and many ducks were not possible to sex. Each observation of an individual duck in one scan is called a notation. The following behaviours were recorded: "foraging", "vigilant", "resting", "comforting", "locomotion" (swimming, walking or flying), "aggression" or "sexual behaviour". In total, 111 h and 40 min of time budgeting was done and we got 5709 notations of Mallard, 1082 of Pintail, 848 of Gadwall, 5772 of Shoveler, 526 of Garganey, 2158 of Teal and 948 of Wigeon.

When broods were observed, species and approximate age according to Gollop & Marshall (1954) were noted. From these observation it was possible to estimate fledging time and hatching time and start of incubation to get a picture of the phenology of the species.

In the statistical analysis the summed time budget data for each sex of each species in every month each year were regarded as one sample. The ecological differences listed in Table 1 and the population densities and sex ratios in Table 2 and 3 were used as class variables when analysing the relationship between proportion of time spent foraging and the different ecological variables. For these analyses I used Spearman rank correlations. One correlation analysis was made

between proportion of time spent foraging and each class variable for each year, month and sex, thus giving sample sizes equal to the number of species observed in each month and year. The effect of migration distance was not tested on the data from June because no species migrate directly before or after this period. In July determination of the sexes was almost impossible at large distances because males had eclipse plumage. The effect of sex ratio could therefore not be tested on the material from July. No correlation analyses were done for unsexed individuals in June 1986 and 1987, nor for males in July 1987 due to very small samples (<150 notations/month).

Table 3. Observed proportion of males in the populations of the dabbling ducks. In July most ducks was not possible to sex and sex ration was therefore not calculated.

Observerad andel hanar i simändernas populationer. I juli kunde flertalet individer inte könsbestämmas, och könskvoterna kunde följaktligen inte beräknas.

Species Art	1986		1987		
	May	June	April	May	June
Mallard <i>Gräsand</i>	0.90	0.87	0.72	0.90	0.88
Pintail <i>Stjärtand</i>	0.51	0.43	0.92	0.95	0.32
Gadwall <i>Snattherand</i>	0.52	0.73	0.52	0.68	0.83
Shoveler <i>Skedand</i>	0.85	0.95	0.58	0.80	0.80
Garganey <i>Årta</i>	0.98	0.96	–	0.69	0.67
Teal <i>Kricka</i>	0.94	0.97	0.54	0.69	0.86
Wigeon <i>Bläsand</i>	0.89	0.85	0.54	0.66	0.80

Table 4. Predictions and significant observations of correlations between proportion of time spent foraging and the class variables from Table 1, 2 and 3.

Förutsägelser och signifikanta observationer av korrelationer mellan andelen tid ägnad åt furagering och klassvariablerna från tabellerna 1, 2 och 3.

Variable Variabel	Predicted ^a Förväntad	Observed ^b Observerad	r_s^c	Month Månad	Year År	Sex Kön	N ^d
Migration distance Flyttningsavstånd	+	0					
Degree of carnivory Grad av animaliediet	-	0					
Population sizes Populationsstorlekar	- (int.)e } + (exp.)e }	+	0.900	July	87	unsexed	7
Proportion of males Andel hanar	-	-	-0.857	May	86	females	7
			-0.929	May	87	females	7
			-0.893	June	86	females	7

^aPredicted direction of the correlations.
Förutsädd riktning på korrelationerna.

^bDirection of significant correlations ($P < 0.05$).
Riktning på signifikanta korrelationer ($P < 0.05$).

^cSpearman rank correlation coefficient.
Korrelationskoefficient från Spearmans rangordnade korrelationstest.

^dSample sizes (the number of species for each sex, year and month).
Provstorlek (antalet arter av respektive kön för varje år och månad).

^eWith intraspecific interference competition or exploitative competition.
Med konkurrens inom arterna genom interferens eller födoexploatering.

To get a more comprehensive picture of the effects of intraspecific competition correlation analyses were made between both population densities and sex ratios and proportion of time allocated to vigilance, aggressions and movements.

Results

In April, only the earliest species, Mallard and Pintail, had started incubation. In May, also Wigeon, Shoveler and Gadwall had started incubation and Teal and Garganey were just about to do so. Some clutches of the earliest species had hatched in May. In June, at least some clutches of all species had hatched but in all species also some individuals were still incubating. In July the latest clutches had hatched and the earliest broods of all species had fledged.

The significant correlation analyses between time spent foraging and the class variables in Table 1, 2 and 3 are shown in Table 4.

Migration distance

The proportion of time spent foraging was not significantly correlated with migration distance during any period (Table 4).

Diet choice

The proportion of time spent foraging was not significantly correlated with degree of carnivory during any period (Table 4).

Population densities

In July 1987 the proportion of time spent foraging by the unsexed ducks was positively correlated with population densities (Table 4). Since a positive correlation in this case possibly indicates exploitative competition, behaviours associated with interference competition (vigilance, aggressions and movements) were not expected to vary with population densities. Proportion of time spent in aggressive encounters or moving by the unsexed individuals in July 1987 was not significantly correlated with population densities ($r_s = -0.354$, $N = 5$, $P = 0.559$ and $r_s = -0.600$, $N = 5$, $P = 0.285$). There were no observations of vigilance by unsexed individuals in July 1987. In April (1987), however, proportion of time spent in aggressions was positively correlated with population densities for males ($r_s = 0.880$, $N = 6$, $P = 0.021$) and movements was positively correlated for females ($r_s = 0.829$, $N = 6$, $P = 0.042$).

Sex ratios

Proportion of time spent foraging was negatively correlated with the proportion of males in the populations for females in May 1986 and 1987 and June 1986 (Table 4). The proportion of males in the populations is not expected to directly act on proportion of time devoted to foraging but rather to increase proportion of time allocated to behaviours associated with interference. Proportion of time spent moving was, indeed, positively correlated with proportion of males in the populations for females in May 1986 ($r_s=0.775$, $N=7$, $P=0.041$), but vigilance was negatively correlated with the proportion of males in the populations for females in June 1986 ($r_s=-0.775$, $N=7$, $P=0.041$), and no other correlations were significant for the females in May 1986 and 1987 and June 1986. The proportion of time allocated to aggressions did not correlate with proportion of males in the populations for any sex in any period. Vigilance did, however, correlate positively with proportion of males for both females and males in April (1987) and for males in May 1987 ($r_s=0.841$, $N=6$, $P=0.036$; $r_s=0.829$, $N=6$, $P=0.042$ and $r_s=0.964$, $N=7$, $P=0.0005$, respectively), but no corresponding negative effect on foraging time could be detected. The proportion of time spent moving (swimming, walking or flying) did also increase with increasing proportion of males in the populations for males in April (1987) ($r_s=0.886$, $N=6$, $P=0.019$), but decreased for males in June 1986 ($r_s=-0.786$, $N=7$, $P=0.036$).

Discussion

Migration distance

Unexpectedly, species with large migration distances were not forced to spend larger proportion of their time foraging. This may indicate that feeding at staging grounds fully compensates for the greater efforts of long migration among dabbling ducks. Krapu (1981) found that Mallards obtained most of the nutrients needed for reproduction at sites occupied prior to arrival on the breeding grounds.

Diet choice

The diet choice, in terms of degree of carnivory, could not be shown to influence the time budget of the dabbling ducks at Stockviken. One should, however, bear in mind that there may be problems to apply correlation analyses on literature data from all over the world and observations from one small and maybe unique area. We, simply, do not know what diet choice the different species have at this locality. Diet choice is known to vary considerably over the season for dabbling ducks (Cramp & Simmons 1977), and there may be large variation also between localities.

Population densities

A positive correlation between time spent foraging and population density may indicate intensive exploitative competition at large population densities. Such a positive correlation was found for unsexed individuals in July 1987. Species with large population densities thus may be able to locally reduce the densities of their prey. Such a local reduction of the prey density is more likely to occur during the late breeding season because males gather in large flocks during moult. However, flocking may also decrease time spent vigilant (Pulliam & Caraco 1984) and thus make it possible to increase time spent foraging. In fact, no vigilance was observed among the unsexed individuals in July 1987. In earlier periods of the breeding season males were expected to show interference competition (mainly competition for females), but in July only exploitative competition was likely to occur. In April (1987), indeed, the proportion of aggressive encounters increased with population densities for the males and movements increased for the females, but no corresponding decrease in foraging time were observed. The lack of correlations between foraging time and population densities in earlier breeding season may have been a result of simultaneous interference competition and exploitative competition working in the opposite directions.

Sex ratios

The sex ratios influenced the proportion of time allocated to foraging for the females in May (1986 and 1987) and in June 1986. A time conflict is, however, evident only for females in May 1986, where proportion of time moving increased with increasing proportion of males in the populations. In the two other cases (females in May 1987 and June 1986) the different species may have reacted differently to the sex ratio, and, thus, not giving any clear pattern. The fact that females in June 1986, actually, showed a negative correlation between vigilance and proportion of males in the populations is, certainly, surprising. Vigilance did, however, increase as the proportion of males in the populations increased for both females and males in April (1987) and for males in May 1987. Proportion of time moving did also increase with increasing male bias in the sex ratios for males in April (1987), indicating the possibility of intraspecific interference competition in early breeding season. But, there seems only occasionally to be a severe time conflict since foraging time is not always affected. This probably indicates that the time budget is not so restricted for dabbling ducks at this location.

In summary, foraging time among female dabbling ducks was influenced by the proportion of males in the populations during some parts of the breeding season. In July there may also be exploitative competition when population densities are large, causing an increase

in the amount of time allocated to foraging. Both sex ratios and population densities did also affect behaviours associated with intraspecific interference competition. It is illustrative that only the variables that were locally measured in each sampling period were found to correlate with certain behaviours, and even these associations were not constant over the years. This points to some of the problems of generalising regarding ecological properties of species. To conclude, it was shown that intraspecific competition did influence time allocation among dabbling ducks, at least during some parts of the breeding season.

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Sammanfattning.

Variationer i samexisterande simänders tidsbudget.

Effekter av avståndet till övervintringslokalerna, dietval, populationstäthet och könkvot på simänders allokering av tid studerades. Hos djur som har säsongsmässig reproduktion kan allokering av tid och energi förväntas påverka den reproduktiva framgången (King 1974). Andelen tid ägnad åt t. ex. att söka och äta föda kan alltså förväntas återspegla de behov och begränsningar ett djur upplever i en viss situation. Generellt sett ökar ansträngningarna för att hitta föda i samband med energikrävande processer som reproduktion och migration. Naturligtvis påverkar både födans kvantiteter och kvaliteter tiden ägnad åt födosök (Sih 1984, Stephens & Krebs 1986). Även krav att ägna sig åt andra beteenden, såsom att undvika rovdjur eller delta i aggressiva interaktioner eller beteenden associerade med reproduktionen, kan påverka hur mycket tid som är tillgänglig för furagering. Mycket av detta är väl dokumenterat, särskilt för fåglar (se t. ex. Brown & Fredrickson 1987, Austin 1987, Masman et al. 1988, Mace 1989). Ytterst få jämförelser har dock gjorts med arter som har olika ekologiska krav och begränsningar men ändå erfår ungefär samma miljömässiga förhållanden (se dock Bergan et al. 1989).

Simänder uppvisar stora ekologiska likheter, men ändå skiljer sig flera arter på vissa punkter såsom t. ex. avstånd till övervintringsplatser (Perdeck & Clason 1981, Pettersson et al. 1986), graden av territorialitet (Nudds & Ankney 1982), val av habitat (Nudds 1983), val av diet (Swanson & Duebbert 1989, Nudds & Bowlby 1984) och val av boplats (Bengtson 1970, Swanson & Duebbert 1989). Några av dessa skillnader mellan arterna kan förväntas ha effekt på allokeringen av tid till födosök.

Följande förutsägelser kan göras. Längre flyttsträcka till övervintringsplatserna förväntas öka andelen furagering tidigt och sent på häckningssäsongen. En högre andel animalier i födan kan göra en snabbare tillfredsställelse av näringskraven möjlig och därigenom minska furageringstiden (Paulus 1988). Exploativ konkurrens inom arterna kan vid höga tätheter av populationerna lokalt minska bytestätheten så att mera tid måste ägnas åt furagering. Konkurrens inom arterna kan vid höga populationstätheter och/eller skeva könkvoter också leda till mer tid ägnad åt vaksamhet och aggressioner

(Mjelstad & Saetersdal 1988), och därigenom minska andelen tid till födosök.

För att testa dessa förutsägelser insamlades tidsbudgetdata i Stockviken, södra Gotland, under häckningssäsongerna 1986 (maj, juni och juli) och 1987 (april, maj, juni och juli). Samtliga sju i Sverige häckande simandarter tidsbudgeterades samtidigt (gräsand, stjärtand, snatterand, skedand, ärta, kricka och bläsand). Medelavståndet till övervintringsplatserna räknades ut för varje art från kartorna i Peterson et al. (1986) (se Tabell 1). Graden av animalier i dieten för de olika arterna klassades med hjälp av uppgifter från Swanson & Duebbert (1989), Spärck (1974), Olney (1965), Cramp & Simmons (1977), Bartonek (1972) och Danell & Sjöberg (1980) (Tabell 1). Vid denna klassning antogs att amerikansk bläsand *Anas americana* och blåvingad ärta *Anas discors* är ekologiska ekvivalenter till den europeiska bläsanden och ärtan. Den relativa tätheten av populationerna och andelen hannar för varje art kalkylerades från tidsbudgetdata för varje månad och år (Tabell 2 och 3). Vid tidsbudgeterandet noterades följande beteenden; "furagerar", "alert", "vilar", "putsar sig", "förflyttar sig" (simmar, går eller flyger), "aggressiv" eller "sexuella beteenden".

Vid de statistiska analyserna summerades tidsbudgetdata för varje art och kön för varje månad och år. En korrelationsanalys gjordes mellan varje klassvariabel och andelen tid ägnad åt furagering för varje år, månad och kön, vilket gav en provstorlek som motsvarade antalet simandsarter som observerats under perioden i fråga. För att vidare belysa effekterna av konkurrens inom arterna gjordes korrelationsanalyser mellan populationernas tätheter samt könkvoter och andelen tid ägnad åt alerthet, aggressioner och förflyttningar.

Andelen tid ägnad åt alerthet var positivt korrelerad med andelen hanar i populationerna för både hanar och honor i april och hanar i maj 1987. Även andelen förflyttningar ökade för hanar i april samt för honor i maj 1986 med ökad andel hanar i populationerna, men minskade för hanar i juni 1986. I juni 1986 minskade också alertheten med ökad andel hanar i populationerna för honorna. Minskad andel furagering med ökad skevhet i könkvoterna uppvisades följdiriktigt av honor i maj 1987, men också av honor i maj 1987 och till och med av honor i juni 1986 (Tabell 4).

Under den första delen av häckningssäsongen (april) var andelarna tid ägnad åt aggressioner respektive förflyttningar positivt korrelerade med populationsstätheterna. Någon korresponderande minskning i andelen tid ägnad åt furagering fanns däremot inte. Under den senare delen av säsongen (juli) var däremot andelen furageringstid positivt korrelerad med populationsstätheterna, vilket antyder förekomst av exploativ konkurrens om födan inom arterna.

Avståndet till övervintringsområdena och andelen animalier i dieten hade ingen detekterbar inverkan på tidsallokeringen hos simänderna. Det förra beror antagligen på att födotillgången på rastlokalerna längs flyttvägarna är goda för simänderna och de kan följaktligen anlända med ganska god status till häckningsplatserna. De måste heller inte börja bygga upp några energireserver redan i juli. Att dietvalet inte influerade

tidsallokering kan kanske delvis bero på att den grova klassificering av andelen animalier i dieten som analysen bygger på inte på ett riktigt sätt återspeglar simändernas dietval på södra Gotland.

Slutsatsen blir att de lokalt skattade könskvoterna och tätheterna hos populationerna, verkar kunna påverka tidsallokeringen hos simänder, åtminstone under delar av häckningssäsongen.