



Predation risk constrains the plasticity of foraging behaviour in teals, *Anas crecca*: a flyway-level circumannual approach

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The trade-off foragers make between predation risk and feeding efficiency is readily studied in dabbling ducks, which have stereotyped feeding methods, some of which prevent predator detection while others do not. Teals forage mostly with only the bill submerged (eyes above the water surface) in winter, but use a broader foraging repertoire in summer. Given the different environments used by teals over the year, it is likely that such a shift is due to changes in diet, but it may also be caused by differences in predation risk between habitats. However, neither predation risk nor teal behaviour has been studied with consistent methods around the year or throughout any of its flyways. Covering wintering, spring-staging, breeding and moulting sites, we combined focal observations of teals and predator flyover data from seven regions ranging from southern France to northern Sweden. Although not apparent at the scale of days within sites, teals indeed relied more on shallow foraging where predation risk was higher, i.e. at wintering sites. Average foraging depth increased gradually from September to August, i.e. from wintering to breeding sites. Foraging bout length of deeply foraging teals did not decrease over the year, suggesting that it is through selection of foraging technique, rather than by the balance between foraging and interruptions, that birds adjust to predation risk. This study highlights behavioural plasticity in response to contrasting selection regimes within a flyway, in dabbling ducks as well as long-distance migrants in general.

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Predation risk and feeding efficiency are the main components in the behavioural trade-off made by foraging animals (e.g. Stephens & Krebs 1986; Lima 1987; Sutherland 1996). Two mechanisms are commonly proposed to explain why feeding efficiency and predation risk have opposite effects on the behaviour of foragers. First, feeding and vigilance may often be mutually exclusive, because individuals have to lower their head to feed and/or have their vision obstructed by the food, thereby preventing predator detection (e.g. Hart & Lendrem 1984; Lima & Dill 1990; Lazarus & Symonds 1992; Illius & FitzGibbon 1994; Fernandez-Juricic et al. 2004;

but see Lima & Bednekoff 1999 for a different view). Second, foragers may have to expose themselves to collect, handle or ingest food, thereby experiencing greater predation risk than individuals remaining hidden in more protected areas (e.g. Lima et al. 1985). The predation risk–feeding efficiency trade-off has received much attention in avian ecology, as it is often easy to see and study how birds pecking on the ground raise their heads to be vigilant (e.g. Bertram 1980; Thompson & Barnard 1983; Alonso et al. 1994; Saino 1994). Long-distance migrants offer a special challenge to researchers and potentially also a deeper insight into the dynamics of behavioural evolution. This is because many of them experience very different conditions at different times of the year and because they undergo major changes in their physiological status, which affect the constraints influencing trade-off decisions. This implies that site- or season-specific studies run the risk of reflecting only a part of the selection regime and behavioural plasticity that occur under natural conditions. Accordingly, around-the-year studies of foraging behaviour in long-distance migrants are much called for, but they remain exceedingly rare (reviewed in Arzel et al. 2006).

In dabbling ducks (*Anas* spp.), the trade-off between predation risk and feeding efficiency is particularly evident when it comes to foraging methods. These birds feed in a number of distinct modes ranging from dabbling with only the bill submerged to upending with the whole anterior part of the body underwater (Szijj 1965). In winter, ducks preferentially use 'shallow' foraging methods in which the eyes are above the water surface, thereby permitting detection of approaching predators (Guillemain et al. 2000). However, when feeding conditions deteriorate (e.g. because of food depletion) some birds will gradually adopt 'deeper' foraging methods with the eyes submerged (Pöysä 1989; Guillemain & Fritz 2002; Guillemain et al. 2002), which is obviously a more risky technique. A switch to deeper foraging has also been documented in summer, but was more short-term and apparently a response to vertical movements of invertebrate prey within the water column (Pöysä 1989). Hence, the foraging behaviour repertoire of dabbling ducks seems more diverse in summer (Pöysä 1989) than in winter.

The French winter studies documenting a switch to deeper foraging methods in response to food depletion (Guillemain & Fritz 2002; Guillemain et al. 2002) concern a restricted geographical area and a limited number of habitats, whereas most *Anas* species have geographically wide winter ranges comprising a variety of structurally and taxonomically different habitats. Furthermore, they use vast areas and a diverse set of habitats in different biomes along their migration routes as well as on their breeding grounds (e.g. Hughes & Green 2005). Throughout the year and throughout their flyways, dabbling ducks are generally easy to observe in good numbers when foraging, and it is also possible to classify their foraging behaviour at long range without disturbing them.

Dabbling ducks are thus excellent model organisms for studying general decision rules for the trade-off between predation risk and foraging efficiency, particularly because they face different predator communities in different regions at different times of the year. Accordingly,

predation risk may vary strongly over the year and between regions as well as between habitats, theoretically selecting for a dynamic and plastic foraging behaviour. All of this applies to the Eurasian teal (hereafter 'teal'), a common Palearctic species with well-known habitat and dietary preferences (e.g. Cramp & Simmons 1977). Using teal as the focal organism, we did a circumannual flyway-level study of foraging behaviour in relation to predation risk by using a strictly standardized sampling protocol. Specifically, we addressed the following questions.

(1) Does predation risk measured as the frequency of flyovers by avian predators vary over the year and between regions?

(2) Is foraging mode in teal correlated with predation risk? Based on earlier studies (e.g. Pöysä 1987a for teal) and foraging theory we predicted that predation risk and the use of gradually shallower foraging modes should be positively correlated.

(3) Is foraging mode related to intraspecific density? Increased group size may force a larger proportion of the birds to engage in less preferred, riskier, deeper foraging (Pöysä 1987b). Alternatively, because predation risk decreases with increasing numbers of congeners in most animals (Elgar 1989; Roberts 1996; Beauchamp 1998), including teal (Pöysä 1994; Gauthier-Clerc et al. 1998; but see contradictory results in Pöysä 1987b, 1991). Because teal density varies between wintering, staging and breeding sites, we explored the role of this factor in explaining foraging depth.

(4) Are changes in foraging depth over the year associated with variation in behaviour in terms of foraging bout length and duration of interruptions between bouts?

METHODS

We recorded the teals' behaviour with a telescope from a fixed point by focal individual sampling (Altmann 1974), that is, an individual was arbitrarily chosen among foraging birds, and we recorded the length of 10 successive foraging bouts in which the individual used the same foraging method plus the length of the 10 associated foraging interruptions. To avoid unintended selection of individuals involved in one foraging method rather than another, we chose the x th individual, entering the telescope from the left as the latter was moved (where x was an arbitrarily chosen number). We distinguished four classes of gradually deeper foraging methods: (1) bill submerged, (2) head submerged, (3) neck submerged and (4) upending, i.e. the entire anterior part of the body was submerged. Associated average actual foraging depths, according to Thomas (1982) were 4.1, 8.1, 17.1 and 23.8 cm, respectively. We calculated the average length of foraging bouts and the average length of foraging interruptions for each individual. An individual was never sampled more than once a day (different parts of the wetlands were considered successively when many birds were present), and with the exception of some of the boreal breeding lakes, it is also unlikely given the general high turnover in teal populations (Pradel et al. 1997) that individuals were sampled on more than 1 day. We recorded the sex of all

studied birds, and overall teal density by doing regular duck counts every 45–90 min at each site. If two members of a pair are considered together (which was very unlikely to be the case anyway, given the way focal birds were selected), their overall time budget may not be independent (i.e. they feed, move and rest at the same time), but the very structure of their behaviour (i.e. feeding bouts and interruptions), plus the type of feeding methods (i.e. depths) they use may well be different. However, male and female foraging behaviour did not differ significantly (unpublished data); hence data from the two sexes were pooled in the analyses.

The frequency of flyovers by aerial predators (number/min) was determined for each study day by continuous recording of any bird of prey and other potential predators flying low enough over the water body to elicit a response by the ducks. In France and in southern Sweden these were mostly marsh harrier, *Circus aeruginosus*, yellow-legged gull *Larus cachinnans*, and herring gull, *L. argentatus*, all known to cause a strong reaction in dabbling ducks (Tamisier 1972; Fritz et al. 2000). In northern Sweden, white-tailed eagle, *Haliaeetus albicilla*, raven, *Corvus corax*, and hooded crow, *Corvus cornix*, were the most common birds observed disturbing dabbling ducks. Crows did not prey upon teals, but they too made ducks vigilant, and may thus be considered as potential threats by teals, forcing the latter to adjust their behaviour. Birds of all the species listed above, including corvids, were considered under the general 'predator' heading.

Data were collected at 25 sites in six distinct geographical areas (hereafter 'regions') throughout Western Europe (Fig. 1). All sites were selected because of their known local, regional or international importance for teal, and they belong to the same flyway for this species as documented by ringing data (Fransson & Pettersson 2001; Guillemain et al. 2005). Ducks are known to be highly

sensitive to human disturbance (e.g. Blanc et al. 2006), and in particular to hunting (reviewed in Madsen & Fox 1995; Tamisier et al. 2003). To avoid biases linked to potential differences in the level of hunting disturbance between regions, all observations were conducted out of the hunting period and/or in protected hunting-free sites (often in nature reserves).

In western France, we observed wintering teal at four sites in the region of Rochefort on the Atlantic coast (45°56'N, 0°58'W). These ranged from 6.5 to 32 ha, and they were the main day roosts of the area (described in more detail in Fritz et al. 2000). Data from these sites were pooled under the 'Atlantic' region heading and comprise 144 focal samples from 60 study days in November 1995–March 1996 and September 1996–March 1997. Data on flyover frequency by predators were available for 40 of these 60 days. Wintering teals were also studied in the Brenne region, in western France close to Poitiers (46°35'N, 0°20'E), where 49 focal samples were obtained at eight inland lakes (range 5–76 ha) on 30 days in November 2001–February 2002 and September 2002–February 2003. Flyovers by predators were not recorded in the Brenne region. The final wintering site was in the Camargue region, close to Arles in southern France (43°40'N, 04°38'E). Here we used a 16-ha wetland within the Marais du Vigueirat to obtain a total of 155 focal samples on 20 study days in October 2002–February 2003 and in October–November 2003. Predator flyover data were available for 15 of these days.

In early spring we studied teals at the Grand-Mare Reserve (40 ha) and at a nearby hunting pond (0.8 ha), both in the Normandy region, close to Le Havre (49°30'N, 0°06'E). Seventeen focal samples were obtained during 5 days between 14 February and 9 March 2004 (predator flyovers were recorded on all days). Later on in spring, and roughly mid-trip within the flyway, we used the alluvial pasture Vinnö Ångar in the province of Scania, southern Sweden (56°03'N, 14°15'E), hereafter termed the 'Vinnö' region (1.5 ha) to record a total of 74 focal samples and flyover observations of predators on 2, 14 and 23 April 2004.

During the breeding season and the postbreeding moulting season we studied teal on seven boreal lakes in the Umeå area in the province of Västerbotten, north-central Sweden (63°49'N, 20°15'E). Six lakes were typical boreal breeding lakes for teal: they were small (2.7–7 ha), oligotrophic, surrounded by coniferous boreal forest, and their shores consisted mainly of floating peat bog (chiefly *Sphagnum* spp.). Data from these six lakes were pooled under the general heading 'breeding lakes' and comprise 29 focal samples recorded on 13 days in June–July 2003 and in July 2004. The frequency of flyovers by predators was recorded on 5 of these days. The seventh studied lake in this region, Brånsjön, is much larger, eutrophic, surrounded by cereals and hayfields, and is situated in an open agricultural landscape. Brånsjön is used as a staging site by thousands of dabbling ducks in spring, and by hundreds for breeding and moulting. Data from this lake were analysed separately under the 'Brånsjön' heading: 292 focal samples were recorded on 36 days in May–July 2003 and in May–August 2004. Predator flyovers were recorded on 32 of these days.



Figure 1. Study regions within the flyway of teals in Western Europe.

As each focal bird used only one foraging method, and because only four methods were considered here, all original foraging data were classified and thus non-normally distributed. To analyse trends over the year, we therefore computed the average foraging depth based on the relative number of birds using each foraging method, i.e. depth per 10-day period starting 1 September (Pöysä 1989), a continuous variable. This variable was normally distributed (Kolmogorov–Smirnov test: $D = 0.11$, $N = 31$, $P > 0.20$). When periods of study overlapped between sites (Table 1), data from those sites were pooled to compute average teal foraging depth, behaviour parameters and predator flyover frequency per 10-day period. For biological reasons we considered the year to start in the beginning of September; winter is not a ‘waiting’ interperiod but, rather, the phase during which dabbling ducks start preparing for the next breeding episode (see also Tamisier et al. 1995).

RESULTS

Foraging Depth Across Regions

The average frequency of flyovers by predators differed greatly between study regions (ANOVA: $F_{5,94} = 16.78$,

$P < 0.0001$). Bonferroni-adjusted t tests at $P < 0.05$ showed that the Atlantic region had a higher value than all others except the Camargue, which itself had a higher value than Brånsjön (Fig. 2a). Other differences between regions were not significant. The average foraging depth of teals also differed significantly between study regions ($F_{6,753} = 45.17$, $P < 0.0001$; Fig. 2b). Among the three regions with more than 5 days of predator flyover data (Atlantic, Camargue and Brånsjön), there was an obvious pattern of teals relying on shallower foraging techniques as predation risk increased (Fig. 3).

Intra-annual Variation in Foraging Depth

The number of focal samples per 10-day period ranged from zero to 70. We excluded the three periods with no or one sample from further analysis (Table 1). Starting with the first 10-day period in September, there was a clear pattern of increasing foraging depth over the year, a relation best fitted by a quadratic decelerating function ($Y = 6.82 + 0.62X - 0.01X^2$, $R^2 = 0.60$, $F_{2,28} = 20.74$, $P < 0.0001$; Fig. 4a). Over the same period, the frequency of flyovers by predators showed a clear decreasing trend ($Y = 0.115 - 0.007X + 0.001 X^2$, $R^2 = 0.85$, $F_{2,27} = 75.76$, $P < 0.0001$; Fig. 4b), as did average teal density (birds/ha;

Table 1. Number of focal samples collected per region and 10-day period (starting 1–10 September)

10-day period	French Atlantic coast	Brenne	Camargue	Normandy	Vinnö	Brånsjön	Breeding lakes	Total
1	2							2
2	6							6
3	11	1						12
4	16	7	11					34
5	6	1	9					16
6	13	3	1					17
7	11	1	8					20
8	7	2	4					13
9	9	4	10					23
10	8	3	2					13
11	6	1	18					25
12		4	16					20
13		2	20					22
14	8	1						9
15	7	4	2					13
16	9							9
17	9	13	41	5				68
18	7	2	13	2				24
19	8			10				18
20								0
21	1							1*
22					29			29
23					19			19
24					26			26
25								0
26						70		70
28						8		8
29						8		8
30						32	7	39
31						57	4	61
32						11	7	18
33						35	8	43
34						32	3	35
35						39		39

*Excluded from analysis because of the small sample size.

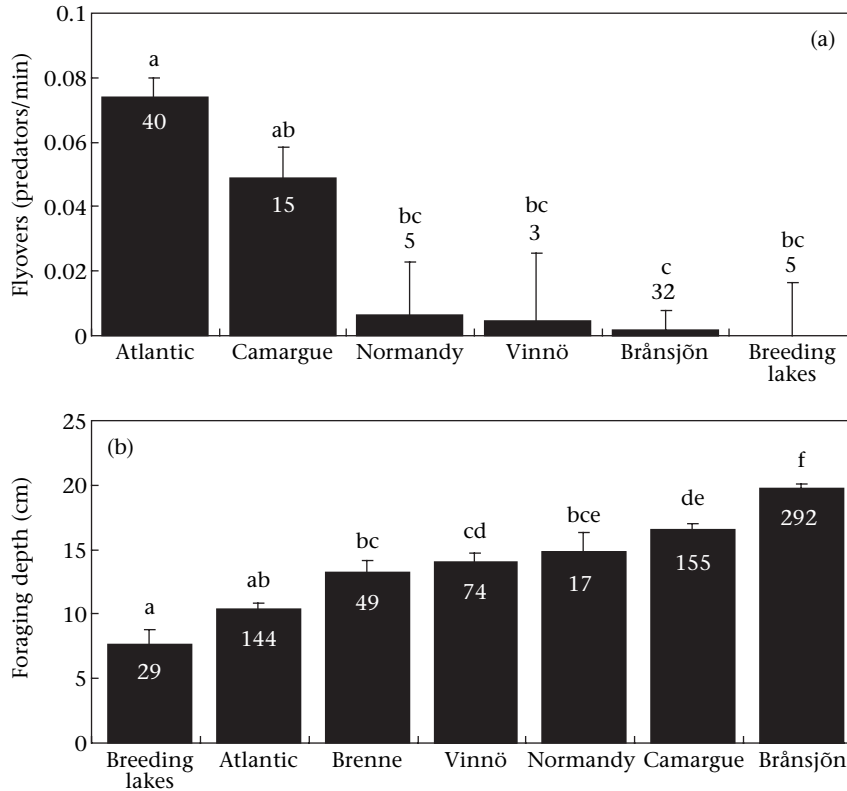


Figure 2. Mean + SE (a) frequency of flyovers by predators and (b) foraging depth of teal in the study regions. Numbers are sample sizes, i.e. number of (a) study days and (b) individuals. See main text for statistics. Columns with different letters differ significantly according to Bonferroni-adjusted posthoc *t* tests at $P < 0.05$.

$Y = 16.06 + 0.44X - 0.03X^2$, $R^2 = 0.33$, $F_{2,29} = 7.25$, $P = 0.003$; Fig. 4c). When we examined variation in foraging depth in relation to predation risk and/or teal density, the full general linear model with these two explanatory factors fitted the data very well ($R^2 = 0.66$, $F_{2,27} = 25.90$,

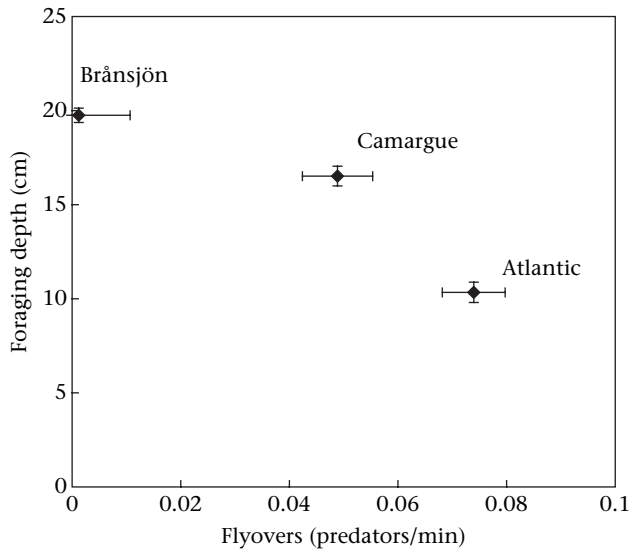


Figure 3. Relation between average frequency of flyovers by predators (predators/min ± SE) and average foraging depth of teals ± SE in Brånsjön, the Camargue and the Atlantic regions.

$P < 0.0001$). An analysis of the partial contributions to the model fit revealed that 91.6% of the variance in foraging depth was, however, explained by changes in the frequency of flyovers by predators alone, which therefore had a highly significant effect ($P < 0.0001$). The contribution of changes in teal density, conversely, did not add significantly to the model fit although the result approached significance ($P = 0.099$).

At the scale of regions, there was no significant correlation between predation risk and average foraging depth (based on the three regions with at least five 10-day periods with such data; Spearman rank correlation: Atlantic: $r_s = 0.007$, $N = 16$ 10-day period averages, NS; Camargue: $r_s = 0.193$, $N = 12$ 10-day period averages, NS; Brånsjön: $r_s = 0.133$, $N = 9$ 10-day period averages, NS).

Associated with the above change in foraging depth, the average duration of foraging bouts decreased over time, also starting 1 September ($Y = 4.79 - 0.10X$, $R^2 = 0.32$, $F_{1,30} = 14.12$, $P = 0.0007$; Fig. 4d). In contrast, the average length of interruptions between foraging bouts did not show any significant trend over time ($R^2 = 0.002$, $F_{1,30} = 0.06$, $P = 0.81$; Fig. 4d). However, when the analysis was restricted to the focal samples of birds using one of the three ‘risky’ foraging methods with the eyes underwater, neither foraging bout duration nor that of foraging interruptions showed a significant trend over time (foraging: $R^2 = 0.01$, $P = 0.56$; interruptions: $R^2 = 0.01$, $P = 0.54$).

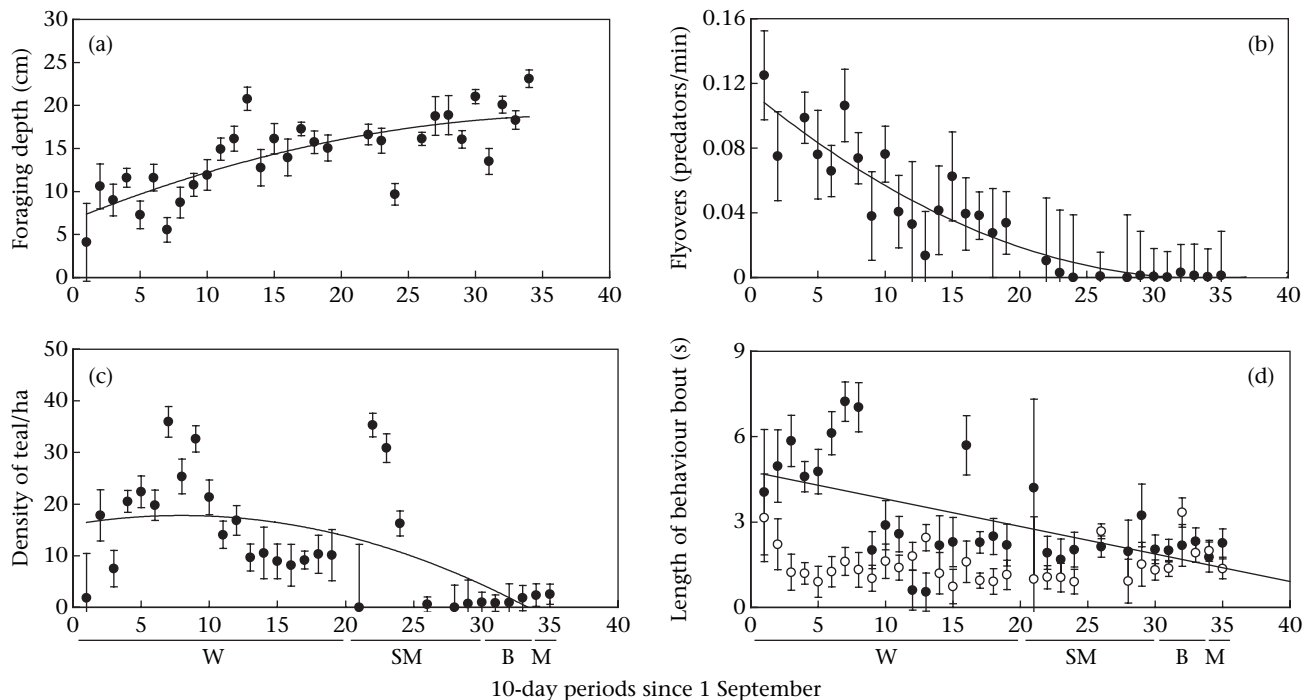


Figure 4. Mean intra-annual variation \pm SE in (a) foraging depth of teals, (b) frequency of flyovers by predators, (c) teal density (individuals/ha) and (d) length of feeding bouts (\bullet , $-$) and feeding interruptions (\circ), expressed per 10-day period starting 1–10 September. See main text for statistics. W: wintering; SM: spring migration; B: breeding; M: moult.

DISCUSSION

Foraging Depth Across Regions

For a long time the dabbling duck guild has been used in community ecology as a textbook example of niche segregation. Accordingly, each species has been supposed to have a rather well-defined foraging depth correlated with its morphology, for example those with a longer body being more likely to forage deeply (Lack 1971; Thomas 1982; Pöysä 1983; Pöysä et al. 1994; Green 1998). However, some studies have documented flexible foraging behaviour in dabbling ducks in summer (e.g. Danell & Sjöberg 1982; Pöysä 1986, 1989), and Guillemain et al. (2002) showed that some species adjust foraging depth in winter by gradually adopting deeper techniques in response to food depletion at the expense of antipredator vigilance. These findings, in combination with the present results, strongly indicate that foraging niches should not be considered as definitive and stable in dabbling ducks. This point is further strengthened by the fact that all our study regions except the boreal breeding lakes hosted four to seven *Anas* guild members when data were collected. In other words, the changes in foraging depth in teals cannot be attributed to a short-term competitive release within the guild. We argue that the behavioural plasticity now evident makes the ecology of these and related bird communities far more complex and challenging than the rather stereotyped view featured in many earlier texts (e.g. Lack 1971).

Guillemain et al. (2002) found that wintering teals switched food types rather than foraging depth (although other species, e.g. mallard *Anas platyrhynchos*, do switch

foraging depth), always using foraging methods in which the eyes were above the surface. This does not contradict the view that foraging depth is a plastic behavioural trait; it implies only that teals avoid risky foraging methods when possible, or when potential costs are too high, as seems to have been the case in winter in the present study. Data from the marshlands of western France may, however, be unrepresentative because this area hosts many raptors: 150 pairs of marsh harrier breed and 500 individuals winter (Nicolau-Guillaumet 1991; Bavoux & Burneleau 2004). Although effective predation is rare, marsh harriers often disturb teals and other ducks at day roosts while looking for sick or wounded individuals (Fritz et al. 2000).

Having studied teals throughout the year and in six geographically distinct regions within the flyway, we anticipated, and found, significant variation in predation risk. Flyovers by predators were more frequent in the wintering regions for which data were available than in any other region. We see three possible explanations for this. First, marsh harriers may be more likely to live close to each other in winter than in summer, as they generally become more or less territorial when breeding (marsh harriers generally breed in loose colonies and hunt solitarily, Newton 1979). Although home range size of individual harriers may not differ between winter and summer (Sternalski 2005), the regional density may be higher in winter simply because of transient birds (see the difference between the numbers of wintering and breeding individuals in western France above). Second, the frequency of flyovers by marsh harriers increases with increasing density of ducks because the probability of finding a sick or wounded individual is higher in larger duck flocks

(Fritz et al. 2000). The observed pattern of higher predator activity on wintering than on breeding grounds thus matches the observed difference in teal density between these two types of regions. Third, in summer it may be more profitable for marsh harriers and other birds of prey to rely on more densely occurring prey than ducks, a switch potentially releasing teals from predation and permitting a greater variety of foraging behaviours. Marsh harriers, in particular, are known to be opportunistic, and to gather readily at temporarily abundant food sources (Ferguson-Lees & Christie 2001). In summer, male marsh harriers provide most of the food to the female and the young, and males are known to forage on small and predictable prey, especially rodents and similar species (Ingenbleek et al. 2004). In conclusion, based on data from the three regions with rather precise estimates of predation risk (i.e. more than 5 days of flyover data), our study supports the hypothesis that teals rely consistently on shallower foraging methods at sites where predation risk is higher, that is, the wintering grounds. Obviously this is a correlative pattern that requires further study to establish causation.

Foraging Depth Over the Year

To our knowledge, this is the first time the foraging behaviour of a long-distance migratory bird has been studied in such detail throughout the year and throughout its flyway. Unlike previous single-site studies of teals (Guillemain et al. 2002), the present analysis revealed a distinct pattern of increasing foraging depth from the arrival at the wintering grounds until the end of the breeding season the next year. The reasons for this may need further examination, and we do not argue that predation risk alone was responsible for this change. Rather, the timing of the behavioural change matches well with the known switch from a granivorous winter diet to a more carnivorous regime immediately before and during the breeding season (e.g. Olney 1963; Tamisier 1971; Thomas 1982; Euliss & Harris 1987 for the American *A. crecca carolinensis* subspecies). Although teals may eat some emerging insects, chironomid larvae form the bulk of the diet of adults in summer (e.g. Danell & Sjöberg 1980), thus probably necessitating the use of deep foraging to reach them at the bottom of water bodies (Danell & Sjöberg 1982; see also Johnson 1995 for the same pattern in *A. crecca carolinensis*). Conversely, when granivorous in winter, teals need only to submerge the bill to reach seeds that float and accumulate along the shores (Thomas 1982). Whether the change in foraging methods we observed was concomitant with, and may be caused by, a change in diet remains to be established. Direct analyses of gut samples may be ethically difficult to carry out, given the fact that this species is not hunted from late winter to late summer in Europe. However, recent developments in the analysis of multiple isotopes in blood, particularly carbon and nitrogen (e.g. Hobson & Clark 1992a,b), may allow a crude determination of food types over the year. It is most unlikely that the behaviour of teals was governed by a combination of food availability at different

depths and the topology of wetlands, that is, availability of feeding areas at various foraging depths. Although data describing this were not available, an earlier analysis in western France conversely revealed that while teals stuck to shallow foraging through the winter, mallard gradually relied on deeper zones of the same water bodies (i.e. these deep areas existed and were available), and continued to exploit throughout the year the same food resources that teals used earlier on in shallow areas (i.e. these seeds were not depleted in deeper areas; Guillemain et al. 2002).

Foraging depth increased over the year corresponding to decreases in both predation risk and intraspecific density (Figs 3, 4). However, the general linear model showed that foraging depth was only marginally related to teal density, whereas predation risk was highly significant. We acknowledge, though, that competition for mates, nest sites and other resources may occur, but we think this is unlikely to affect foraging behaviour. Similar responses have been observed in other species, where foraging behaviour was adjusted to changes in predation risk (e.g. Milinski & Heller 1978; Lima 1985; reviewed in Lima & Dill 1990; Sih 1993). There is an important difference of scale between these studies and ours, though: in the former there were generally on-site short-term responses, whereas we found no such correlation between foraging depth and predation risk. We hypothesize that teals in our study instead responded to predation risk at a more general level, avoiding risky foraging methods at risky sites where there were more predators, and adopting a wider behavioural repertoire at safer sites and during periods when dietary demands made it necessary. Similarly, Pöysä (1989) showed that teals switched foraging methods during the course of a morning in response to the vertical downward movement of invertebrate prey, a behaviour that high predation risk in winter would not favour. Furthermore, given the fact that the predators considered here, especially the marsh harrier, rely on surprise as a hunting technique (Schipper et al. 1975), it may effectively be too risky for teals to adjust their behaviour too quickly to that of the predators, for example at the scale of days. Teals may generally avoid foraging with the eyes underwater in winter, preventing any detection of an approaching predator (Pöysä 1987a), because wintering sites are always risky, even if on some particular days the frequency of flyovers by predators may be low. We do not rule out the possibility that teals responded to the density of congeners within a certain radius (i.e. group size; Pöysä 1994) rather than to the average density of birds on the entire wetland, which may explain the poor correlation we observed with individual behaviour. However, a preliminary analysis including teal number instead of teal density in the model did not fit the changes in foraging depth better, and its effect was not significant (1.7% of the variance explained, partial $P = 0.519$). We could not analyse the effect of proper group size (i.e. number of close neighbours) and this would require specific data recording in future behavioural studies.

We found that switching from shallow to deep foraging was generally associated with shorter foraging bouts (Fig. 4d; see also Guillemain et al. 2001). However, the

most interesting underlying aspect of this pattern is that teals foraging deeply, that is, with the eyes underwater, did not change either foraging bout length or the duration of foraging interruptions over time. The fact that foraging bout length did not decrease when riskier foraging methods were adopted suggests that it is through the selection of foraging technique rather than the balance between foraging and interruptions (when birds can be vigilant) that teals adjust to predation risk. These results are different from those of Pöysä (1987a), who hardly ever observed teals switch to safer foraging methods when predation risk was higher, but instead noted that they increased the length of interruptions between foraging bouts to be more vigilant. The timescale in Pöysä's study was different from ours, though; he considered the actual presence of a predator at the moment duck behaviour was studied, while we considered averages over a few days.

Conclusion

Most behavioural studies of migratory birds are conducted within a single site or area, within a season, or both. Dabbling ducks are no exception to this pattern, and, furthermore, the majority of studies are from either wintering or breeding sites. The paucity of behavioural studies of ducks on migration stopover sites and the lack of circumannual flyway-level approaches are critical gaps in our knowledge (Arzel et al. 2006). The present study fills this gap with respect to foraging behaviour in teals and provides links between results of earlier studies: teals have been observed to rely on both shallow and deep foraging methods on their breeding grounds (Danell & Sjöberg 1980, 1982; Pöysä 1987a, 1989; Johnson 1995), while earlier winter studies have documented a rather limited behavioural repertoire mainly comprising shallow foraging methods (termed 'dabbling', 'grubbing' or 'dibbling', e.g. Tamisier 1972; Thomas 1982). As we have used strictly standardized methods throughout the flyway to record a proxy for predation risk, we argue that a relaxation of predation risk in summer permits a wider repertoire of foraging behaviours, especially as observed foraging depth could not be explained by between-region differences in wetland basin shape (cf. Nudds et al. 2000). All of this puts the focus on behavioural plasticity as a response to contrasting selection regimes within the flyway, in dabbling ducks as well as in long-distance migrants in general. More flyway-level circumannual studies are needed if we aim at a better understanding of the factors limiting populations and structuring communities.

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