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REVIEW

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Ecology of spring-migrating Anatidae: a review

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Abstract Spring migration is generally considered as a crucial period of the year for many birds, not the least due to its supposed importance for subsequent breeding success. By reviewing the existing literature for Anatidae (ducks, geese, and swans), we show that little is known about their ecology in spring, although some goose species are exceptions. Another general pattern is that the ecology of Anatidae at staging sites is particularly neglected. Existing studies tend to focus on questions dealing with acquisition of nutrient reserves, whereas almost nothing has been published about stopover habitats, time use, microhabitat use, foraging behaviour, food availability, food limitation, diet selection, and interspecific relationships. Besides summarising present knowledge, we identify taxonomic groups and topics for which gaps of knowledge appear the most evident, thereby also highlighting research needs for the future.

Keywords Anatidae · Ducks · Review · Spring migration · Staging

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Introduction

Stopover ecology is one of the least studied aspects of avian migration (Lindström 1995). This is equally true for fall and spring, and it is also the case for the otherwise well-studied Anatidae (e.g., swans, geese, and ducks) notwithstanding some early calls for a more profound understanding of factors influencing migration sensu latu (e.g. Lebret 1947). The avian literature as a whole abounds with examples showing that activities during the pre-nesting period may have general and profound effects on subsequent breeding success and other fitness-related measures, such as survival. Some studies indicate that this may be generally true for waterfowl too, i.e. that spring is indeed a critical period (e.g., Ankney and MacInnes 1978; Ebbinge et al. 1982; Hepp 1984; Hohman et al. 1988; Zimin et al. 2002). However, to date there has not been any comprehensive review to evaluate this.

Many Anatidae breed in temperate or sub-arctic climes, and they are generally early migrants. This means that spring migration, also called 'prenuptial' or 'return migration' (Anonymous 1979, 2001), and staging generally take place during a very 'lean' time of the year. More specifically, an energetically costly flight is undertaken when food resources are often still scarce along the migratory route as well as on the breeding grounds at the time of arrival. Several studies have highlighted this proximate and adaptive dilemma, which may be equally relevant for early-migrating temperate species as it is for arctic breeders (e.g. Ebbinge et al. 1982; Thomas 1983; Newton 2004). Furthermore, birds not only have to make it to the breeding grounds; remaining nutritional reserves and food availability at arrival may have important effects on fecundity and other aspects of fitness (e.g. Daan et al. 1986; Krapu and Reinecke 1992; Drent et al. 2003).

The conceptual framework dealing with strategies and trade-offs in securing nutritional demands for spring migration and breeding broadly classifies birds as being either 'capital' or 'income' breeders (Drent and Daan 1980; Bonnet et al. 1998). Generally speaking, capital breeders prepare for reproduction by storing energy reserves well ahead of clutch formation, whereas income breeders rely on food obtained on the breeding grounds to produce their young. Geese are supposed to be proper capital breeders (Clausen et al. 2003), even if some species may rely on both strategies depending on individuals (Klaassen 2002). Given their relatively low body mass, ducks (Anatinae) should theoretically all be income breeders (Meijer and Drent 1999; Klaassen 2002), especially the smallest species like the green-winged teal *Anas carolinensis* (Paquette and Ankney 1998). This implies that ducks rely largely on food at staging sites to fuel their migration flight, and on food on the breeding grounds to breed (Ankney et al. 1991; Alisauskas and Ankney 1992a). However, there has not been any literature review to evaluate the generality of these patterns and assumptions.

There are indeed studies of Anatidae species addressing key topics such as the role of exogenous resources for migration and breeding, how conditions during migration influence breeding success, and, if so, which stage or time-phase is the most crucial for this connection. However, there is no synthetic view of the link between spring migration and breeding success.

Focussing on temperate European and North American species we here set out to: (1) review the available literature about spring-migrating and pre-nesting Anatidae in order to identify general ecological patterns, (2) identify critical knowledge gaps for this time of the year, and (3) outline research needs for the future. We have included scientific studies treating the 'time window' from the departure from wintering grounds to the onset of nesting. Most of the sources used are published in peer-reviewed journals or in books, but we acknowledge the fact that some valuable information in national and regional sources may be missing.

Timing of spring migration

Although most Anatidae species are early migrants compared to many other birds, departure date and duration of spring migration vary considerably (Table 1). The significance of this timing has been demonstrated for some geese, especially in terms of the effects on subsequent breeding success (e.g. Summers and Underhill 1987; Bromley and Jarvis 1993; Budeau et al. 1991; Fox 2003). Such a causal link has been shown in only a few ducks, but it is unclear whether this is because it does not exist or because it has not been properly looked for (e.g. Newton 2004; Esler and Grand 1994). General information on spring migration periods for Anatidae is found in faunistic and reference sources (see also Anonymous 2001), but the precise timing is still unknown for many populations, at least in Europe. The use of large-scale long-term sets of ringing recovery data (e.g. http://www.euring.org/edb/index.htm) can help to fill this gap (Guillemain et al. 2006).

The duration of spring migration varies among species, but also between populations and among individuals within a species (Table 1). The latter may be due to individual differences in body condition and related 'decisions' about when, where and for how long stopover sites are used. Virtually all Anatidae stage at stopover areas along the migration route to rest and/or feed (e.g. Guillemain et al. 2004). Refuelling patterns, in turn, may influence in which body condition individuals arrive at breeding grounds, a topic treated below. Consequently, environmental conditions at stopover sites may act as a proximate factor affecting body condition at the onset of breeding, and possibly the outcome of nesting activities (e.g. Blokpoel and Richardson 1978; Ebbinge and Spaans 1995).

Disturbance

Survival and reproductive output are directly and positively related to body condition in some Anatidae (e.g., Féret et al. 2003). Factors affecting nutrient storage a few weeks prior to nesting may thus have significant impact on breeding performance, hence on recruitment and population growth. In other words, pre-breeding Anatidae are potentially sensitive to disturbance reducing their ability to forage and rest, or increasing the expenditure of already stored reserves.

Indeed, disturbance does affect geese and ducks (Madsen 1995). Escape flights are costly in their own right (Madsen 1998; Riddington et al. 1996), frequently forcing birds to spend more time vigilant at the expense of foraging activities (Fox et al. 1993; Riddington et al. 1996). Disturbance may also lead to an increased utilization of less disturbed but also less profitable habitats (Mathers and Montgomery 1997). However, most studies of disturbance concern fall and winter (Madsen 1995). There is thus a need for research explicitly focussing on migrating and spring-staging birds (see Skyllberg et al. 2005).

The main disturbance agents appear to be man and predators, especially diurnal raptors (Fritz et al. 2000). Human disturbance may arise from recreational activities like boating and hunting (Matthews 1982; Korshgen et al. 1985; Stock 1993; Madsen 1995; Féret et al. 2003; Schummer and Eddleman 2003), and also from agriculture, industrial works, and transportation (Skyllberg et al. 2005). There are only a few studies explicitly addressing the effects of human disturbance on energy expenditure in migrating waterfowl (Féret et al. 2003; Schummer and Eddleman 2003), and it is only recently that a negative effect on fat storage and subsequent breeding success was demonstrated in geese (Drent et al. 2003; Béchet et al. 2004).

The immediate consequences of hunting on staging migrants remain poorly investigated, while the impact

Table 1 Spring departure dates of some Anatidae taxa. Nomenclature follows Anonymous (2001) and Delany and Scott (2002)

Taxon	Breeding area	Wintering area	Onset of migration	Reference
Mute swan *Cygnus olor*	Temperate Europe and Asia	W Europe, Mediterranean Sea	Late January	Anonymous (2001)
Pink-footed goose *Anser brachyrhynchus*	Svalbard	Denmark, Netherlands, Belgium	Mid January*, early April**	Anonymous (2001)*, Madsen (2001)**, Drent et al. (2003)
	E Greenland and Iceland	England and Scotland	Late March	Anonymous (2001)
Greater white-fronted goose *A. albifrons albifrons*	Kanin Peninsula in N Russia E to Kolyma River	NW, C and E Europe	Late January	Anonymous (2001)
Greenland white-fronted goose *A. a. flavirostris*	W Greenland	Ireland, Scotland, Wales	Mid April	Fox and Madsen (1981), Fox et al. (1983), Fox (2003)
Greater white-fronted goose *A. a. frontalis*	E Siberia	E Asia	March	Amano et al. (2004)
	C and NW Alaska across arctic Canada	Louisiana, Texas and Mexico	March	Krapu et al. 1995
Lesser white-fronted goose *A. erythropus*	N Scandinavia, arctic W Russia	SE Europe, Caspian	March	Bellrose (1978)
Tundra bean goose *A. f. rossicus*	N Siberia	W and S Europe	late January	Anonymous (2001)
Taiga bean goose *A. f. fabalis*	N Fennoscandia, N Russia and W Siberia	Poland, E Germany, S Sweden, Denmark and Netherlands	Early February	Anonymous (2001)
Lesser snow goose *Anser c. caerulescens*	W Hudson Bay, Southampton Is, Baffin Is	Gulf of Mexico coast	March	Thomas (1983), Ganter and Cooke (1996), Klaassen (2002)
	C Canadian arctic	S USA, N Mexico	Early April	Ebbinge et al. (1982), Owen and Black (1990)
	Wrangel Is, Russia	California, Mexico	April	Zacheis et al. (2001)
Greater snow goose *Anser c. atlanticus*	E high arctic Canada, NW Greenland	E USA	Late March	Gauthier et al. (1984, 1992), Choinière and Gauthier (1995), Giroux and Bergeron (1996)
Canada goose *Branta canadensis interior*	N Ontario W of James Bay and S Hudson Bay	Wisconsin Illinois	Mid March	Gates et al. (2001)
Cackling canada goose *B. c. minima*	Yukon-Kuskokwim Delta, Alaska	W Oregon, W Washington	April	Zacheis et al. (2001)
Taverner canada goose *B. c. taverneri/parvipes*	Interior Alaska	Washington to California	April	Zacheis et al. (2001)
Giant canada goose *B. c. maxima*	Canada between lakes Winnipeg and Manitoba	Mississippi flyway	Early April	McLandress and Raveling (1981a, b)
Barnacle goose *B. leucopsis*	Svalbard	SW Scotland	Late April	Pettifor et al. (2000)
	N Russia, E Baltic	N Germany, Netherlands	April	Bellrose (1978)
Dark-bellied brent goose *B. bernicla bernicla*	W Siberia	Coastal W Europe	February	Ebbinge et al. (1982), Teunissen et al. (1985), Pettifor et al. (2000), Van der Wal et al. (2000), Anonymous (2001)
Light-bellied brent goose *B. b. hrota*	Svalbard, N Greenland	Coastal Denmark, NE UK	March	Van der Wal et al. (2000), Clausen et al. (2003), Anonymous (2001)
Black brant *B. b. nigricans*	Low arctic N America	E Pacific coast, mainly Mexico	Mid February	Derksen and Ward (1993)
Wood duck *Aix sponsa*	E North America, W Cuba	Partial migrant S Mexico	Early February	Dugger and Frederickson (1992)
Eurasian wigeon *Anas penelope*	W Siberia and NW, NE Europe	NW Europe	February	Jacobsen (1989), Anonymous (2001)
Gadwall *A. strepera*	S Canada and Alaska, N USA	S and W N America, Mexico	March	Dwyer (1975), Paulus (1984), Ringelman (1990), Ankney and Alisauskas (1991)
	Scandinavia, Baltic States and Eur Russia	W Europe	Late January	Anonymous (2001)

Table 1 (Contd.)

Taxon	Breeding area	Wintering area	Onset of migration	Reference
Common teal *A. crecca*	N Europe	NW Europe	Late January* early February**	Anonymous (2001)*, Guillemain et al. (2006)**
Green-winged teal *A. carolinensis*	Alaska, Canada, NW USA	USA, Mexico, Caribbean	February	Bellrose (1978)
Mallard *A. platyrhynchos*	N Europe	NW Europe E to the Baltic	Mid January*, February**	Anonymous (2001)* Asplund (1981)**, Robinson et al. (2003)
	Alaska, Canada, USA	SW and S Canada, USA	February	Bellrose (1978), Krapu (1981), Jeske (1996), Dugger (1997)
American black duck *A. rubripes*	E Canada, NE USA	E USA and Canada	Mid February	Coulter (1955), Bellrose (1978), Owen and Reinecke (1979), Longcore et al. (2000)
	C Canada, N USA	Mississippi flyway	Early February	Bellrose (1978), Owen and Reinecke (1979)
Northern pintail *A. acuta*	NE Europe	Medit Basin and Sahel region	Late January	Anonymous (2001)
	Baltic States, Fennoscandia and Iceland	NW Europe	Early February	Anonymous (2001)
	Alaska, Canada, N USA	SW Canada, USA, Mexico, Caribbean, C America	Early February	Fredrickson and Heitmeyer (1991)
Blue-winged teal *A. discors*	N America	S USA, C America, N South America	Mid January	Taylor (1978), Gammonley and Fredrickson (1995)
Cinnamon teal *A. cyanoptera*	W Central N America to NW Mexico	SW USA, Mexico, C America	February	Gammonley (1995)
Northern shoveler *A. clypeata*	N Europe, Mediterranean Basin	Fennoscandia and Russia	Early February	Anonymous (2001)
	Alaska, Canada, N USA	SW Canada, USA, Mexico, C America	Late March	Afton (1979), Ankney et al. (1991), DuBowy (1996)
Garganey *A. querquedula*	W Eurasia	Africa, S of Sahara	February	Anonymous (2001)
Red-crested pochard *Netta rufina*	N Black Sea to c. 90°E	Iberia across S and C Europe to W and C Asia	Late January	Anonymous (2001)
Redhead *Aythya americana*	Alaska, W and S Canada, W USA	W, S and SE USA, Mexico	Early March	Custer (1993)
Common pochard *A. ferina*	W Eurasia	S to N Africa and the Gulf, small numbers in W and NE Africa and Arabian Peninsula	Late January	Anonymous (2001)
Tufted duck *A. fuligula*	Iceland, Fennoscandia, Baltic region and Russia east to 65°E	Baltic and N Sea and Atlantic coasts	Late January	Anonymous (2001)
Greater scaup *A. marila*	Iceland	Ireland and Scotland	Late February	Anonymous (2001)
	Fennoscandia and N Russia	Baltic Sea, N Sea and Atlantic S to France	February	Anonymous (2001)
Common eider *Somateria mollissima*	Coasts of N Europe, including Baltic Sea	S Baltic and North Sea	February	Anonymous (2001)
Long-tailed duck/ Oldsquaw *Clangula hyemalis*	Fennoscandia, N Eur Russia and W Siberia	Baltic Sea, Wadden Sea	Mid February	Anonymous (2001)
Steller's eider *Polysticta steller*	N Siberian coast	N Norway, SE Baltic	May	Fredrickson (2001)
	N Siberian coast, N and W Alaska	SW Alaska, Aleutians, Kamchatka, Kuril Is	Early May	Fredrickson (2001)
Common goldeneye *Bucephala clangula*	N Europe	Baltic Sea, Denmark, the Netherlands, Britain and Ireland	Early February	Anonymous (2001)
	Alaska, Canada	USA, Atlantic and Pacific coast of Canada and Alaska	Late February	Eadie et al. (1995)
Black scoter *Melanitta nigra*	Fennoscandia and Russia E to river Lena, and Iceland	Baltic Sea and S North Sea, Atlantic seaboard to Morocco	February	Anonymous (2001)

Table 1 (Contd.)

Taxon	Breeding area	Wintering area	Onset of migration	Reference
Velvet scoter *M. fusca*	Fennoscandia E to Siberia	Baltic Sea, Norway, Netherlands, Britain, France and Spain	Late February	Anonymous (2001)
Red-breasted merganser *Mergus serrator*	N Europe and NW Russia	Baltic Sea to Portugal	February	Anonymous (2001)
Common merganser *M merganser*	Fennoscandia and NW Russia	Baltic Sea, North Sea, C Europe and W Mediterranean.	Late January	Anonymous (2001)

on migratory routes and subsequent breeding success has been explored to some extent (Kokko et al. 1998; Francis 2000; Mainguy et al. 2002; Féret et al. 2003; Béchet et al. 2003, 2004). Nowadays hunting generally does not last later than February in Europe and North America, but there are some states and regional exceptions (e.g., in Alaska subsistence harvest season is globally opened from April to August, Manson 2005; snow geese may be hunted in spring in some Canadian provinces, see http://www.cws-scf.ec.gc.ca;; some sea ducks may be hunted in Finland in April–May, H. Pöysä personal communication). However, spring migration starts in January and February in many species (Table 1), which is why it remains essential to study the impact of hunting and other anthropogenic disturbance on staging migrants. For example, the EU wild bird directive (Anonymous 1979) states that ''migratory species (shall not be) hunted during their return to their rearing grounds'', thus making it a priority for policy-making and management to gain more precise knowledge about the onset of spring migration of different populations, including its variability.

Severe disturbance may have far-reaching consequences for staging birds. Geese are known to start using new staging sites in geographically 'untraditional' areas and their entire suite of behaviours may be attuned to local patterns of food availability and disturbance (Drent et al. 2003; Skyllberg et al. 2005). Similarly, Mathers and Montgomery (1997) showed that wigeon *A. penelope* used secondary habitats in order to avoid human disturbance. Such habitat shifts may decrease foraging time and also make diet selection suboptimal. However, brent geese *Branta bernicla* in the same study accepted using rather heavily disturbed areas, which were more energy-profitable. The degree of vulnerability to disturbance may thus vary a lot among species.

For some geese there is convincing documentation that disturbance, behaviour, nutritional status, and breeding success are all linked in a chain of causation. In ducks, though, the evidence is more circumstantial, especially the final link between nutritional status while on staging sites and subsequent breeding success (see below). In other words, it remains unknown if the smaller species obtain all energy needed for reproduction on the breeding sites proper. Nor is it known for any species what is the threshold level above which disturbance has a significant effect on body condition. We see a need for studies relating time use, diet selection, and nutritional status of individuals to different degrees and sources of disturbance. Note also that the effects of predator-induced disturbance remain poorly documented, especially in combination with human disturbance. The paucity of studies of disturbance on spring staging sites and from the pre-nesting period at breeding sites (see, however: Korshgen et al. 1985; Stock 1993; Madsen 1995; Féret et al. 2003; Schummer and Eddleman 2003; Béchet et al. 2004; Skyllberg et al. 2005) is also a fundamental problem because the corresponding behavioural responses in fall and winter may differ from those in birds entering the breeding phase (Bluhm 1992; Fox 2003). For example, bean geese *Anser fabalis fabalis* that are very approachable on wintering sites in southern Sweden, are wary and very easily disturbed on boreal staging sites only 6 weeks later (J. Elmberg, personal observation).

Habitat choice

Migrants have to find suitable habitats for resting and refuelling all along their journey (e.g., Moore et al. 1990), but the impact of environmental change in this context, especially habitat loss, is often difficult to quantify. Year-round models (e.g., Pettifor et al. 2000) are one tool that has proven capable of predicting population decline following habitat loss at wintering and spring-staging grounds, but they need to be developed further. Natural vegetation successions, too, may alter habitats so that they become unsuitable for migrating birds in terms of food availability (Van der Wal et al. 2000). Some Anatidae are more specific in their choice of spring staging habitats, and there have been attempts to characterize which are the most attractive to different species (Heitmeyer and Vohs 1984). Weather conditions in winter and spring often also influence wetland availability, which in turn may influence nesting phenology and success by limiting food resources for pre-nesting and nesting birds (e.g., mottled duck *A. fulvigula*, Grand 1992). Consequently, water conditions in spring are important to breeding success in some species (e.g., mallard *A. platyrhynchos*, Krapu et al. 1983).

We have already pointed out that Anatidae females generally need a lot of exogenous energy the last few weeks prior to incubation, and also that the availability of specific food resources may vary considerably among habitats. Females can respond to such variation by devoting more time to feeding (Dugger and Petrie 2000), and by doing so managing to produce the same clutch size as do females in more productive habitats. However, the trade-off between parental investment and clutch size remains little studied with respect to individual quality and fitness of the young; i.e. whether clutch size is maintained at the cost of duckling size or weight at hatching. Stopover habitats differ quantitatively and qualitatively in food availability, and consequently all birds will not accumulate the same amount of fat (Gauthier et al. 1984).

Migrating birds themselves can also affect food availability, as foraging may impact present as well as future food resources (Zacheis et al. 2001). Short-term food depletion at stopover areas may even be crucial for energy storage in later-arriving individuals (e.g. bewick's swan *Cygnus columbianus*, Nolet and Drent 1998).

Foraging and diet

Little is known about the nutritional dynamics of migrating Anatidae, i.e. the rate at which they accumulate and use energy stores. It appears, though, that most species have to find adequate food at strategic locations along the migration route for continued migration and sometimes also for breeding purposes. If this is generally true, food availability will have proximate and ultimate effects on the timetable, on the route as well as the selection of stopover sites used to replenish reserves (King 1974; Van Eerden 1984).

As a general pattern, the time devoted to feeding activities increases in late winter and early spring (e.g., McLandress and Raveling 1981a; Paulus 1988; Tamisier and Dehorter 1999). This increase in daily food intake rate in pre-migrating birds is supposed to allow them to accumulate enough protein for migration (Lindström and Piersma 1993). However, the entire behavioural suite of spring-staging waterfowl has been studied in only a few species at some specific stopover sites (e.g. steller's eider *Polysticta stelleri*, McKinney 1965; barnacle goose *B. leucopsis*, Black et al. 1991; pink-footed goose *A. brachyrhynchus*, Madsen 1985, Boyd and Fox 1992). Microhabitat use and foraging behaviour in spring-staging ducks are less studied still (but see Arzel and Elmberg 2004; Guillemain et al. 2004). This is surprising and unfortunate, especially in the light of the presumed causal link between migration, nutrient storage, and subsequent breeding success (Swanson et al. 1985; Krapu and Reinecke 1992; Klaassen 2002).

Paulus (1988) found that the bulk of time budget studies of non-breeding Anatidae had been carried out at day for practical reasons, and that very few concern spring stopovers. Some Anatidae, especially dabbling ducks, forage at night in winter (Tamisier and Dehorter 1999), but there is little information about the extent of nocturnal foraging during spring migration. In breeding areas at high latitudes there is continuous daylight and potentially around-the-clock opportunities for foraging. We conclude that time use and behaviour need to be sampled around the clock and around the year if we want to make correct assessments of foraging habits, habitat use, and the relative value of these habitats. As far as we know, such data are not available for any Anatidae, even if studies with different methodologies are combined.

Swans, geese, and ducks have a wide range of diets, from entirely herbivorous to almost completely carnivorous. A shift in spring from a largely granivorous to a largely invertebrate diet is seen in many dabbling ducks (Swanson 1977), but also at this time there are considerable differences among species (Keith 1961; Table 2). Such a springtime diet shift is generally attributed to the needs for egg production (Alisauskas and Ankney 1992a, b) and to cover migration costs (LaGrange and Dinsmore 1988). A shift to more energy-rich food is seen also in species in which adults are pure herbivores, e.g. geese (McLandress and Raveling 1981b; Madsen 1985; Carrière et al. 1999; Gates et al. 2001).

At a first glance, standard references appear to contain a lot of information about waterfowl diets, mainly based on analyses of contents of guts and oesophagi (e.g., Martin and Uhler 1939; Cramp and Simmons 1977; Glutz von Blotzheim 1990). However, studies of birds at spring staging sites or newly arrived on breeding grounds are few or lacking for most species, and those that exist generally represent restricted geographical areas or habitats that are far from representative (e.g., Coulter 1955). Keeping these limitations in mind, the literature tends to support a general pattern of springtime diet shift in dabbling ducks and geese. In addition, the phenology of certain plant foods may affect their availability to also impact the final pre-breeding body reserves in some herbivorous species (Prop and Deerenberg 1991). This suggests a general selective advantage of adjusting migratory pathways and timing to the phenology of major food items, but this has been little studied and rarely demonstrated (Drent 1996).

Eventually, density-dependent effects resulting from food and habitat limitation may influence breeding success (Drent 1996). Jeske (1996) hypothesized that one of the functions of migrating may be to avoid areas with scarce resources or dominant species that could exclude competing subordinates. No study so far has demonstrated interspecific competition related to food limitation in spring staging Anatidae; Arzel and Elmberg (2004) found that community and niche patterns in a guild of spring-staging dabbling ducks were quite similar to those in other seasons.

It must be kept in mind that food may not always be limiting, especially for proper herbivores. Gates et al. (2001) showed for canada geese *B. canadensis interior* in

Table 2 Aspects of nutrient acquisition and diet of some Anatidae taxa. Abbreviations are: endo endogenous, exo exogenous, herb herbivorous, gran granivorous, omni omnivorous, carn carnivorous

Taxon	Breeding area	Wintering area	Time between arrival at breeding sites and incubation	Source of nutrients for repro	Energy store during migration	Diet	Diet shift	Reference
Trumpeter swan *C. buccinator*	Alaska, W Canada	Coast S Alaska, B Columbia and NW USA	2–3 weeks	Endo	Yes	Herb		LaMontagne et al. (2001)
Taiga bean goose *A. fabalis fabalis*	Scandinavia E to W Siberia	NW Europe			Yes	Herb		Nilsson et al. (1999a)
Pink-footed goose *A. brachyrhynchus*	Svalbard	Denmark, Netherlands, Belgium		Endo		Herb	Yes	Madsen (2001), Drent et al. (2003)
	E Greenland, Iceland	Scotland, England		Endo	Yes	Herb	Yes	Fox et al. (1993)
Greater white-fronted goose *A. albifrons albifrons*	European arctic Russia and NW Siberia	NW Europe		Endo and exo	Yes	Herb	Yes	Mooij et al. (1999)
Greenland white-fronted goose *A. al.flavirostris*	W Greenland	Ireland, Scotland, Wales	10–20 days	Exo		Herb	Yes	Fox and Madsen (1981), Fox et al. (1983), Fox (2003)
Greater white-fronted goose *A. al. frontalis*	E Siberia	EAsia		Exo		Herb		Amano et al. (2004)
	Yukon-Kuskokwim Delta, Alaska	Central Valley, California	2–3 weeks	Exo		Herb		Budeau et al. (1991), Carrière et al. (1999)
	C and NW Alaska across arctic Canada		10 days	Endo	Yes	Herb		Bellrose (1978), Krapu et al. (1995)
Tule white-fronted goose *A. al. gambelli*	Alaskan taiga	California, USA		Endo	Yes	Herb		Ely and Raveling (1984, 1989)
Lesser white-fronted goose *A. erythropus*	N Scandinavia, arctic W Russia	SE Europe, Caspian			Yes	Herb		Markkola et al. (2003)
Greylag goose *A. anser*	Iceland	UK, Ireland		Endo	Yes but mainly prior	Herb		Mitchell and Sigfusson (1999)
	NW Europe	NW Europe, SW Europe		Endo	Yes (some individuals)	Herb	Yes	Nilsson et al 1999b
Lesser snow goose *Anser c. caerulescens*	W Hudson Bay, Southampton Is, Baffin Is	Gulf of Mexico coast	Some days	Endo and exo	Yes	Herb/gran	Yes	Bellrose (1978), Thomas (1983), Alisauskas and Ankney (1992a), Ganter and Cooke (1996), Klaassen (2002)
	C Canadian arctic	S USA, N Mexico	Some days	Endo and exo	Yes (fat)	Herb	Yes	Bellrose (1978), McLandress and Raveling (1981a, b), Ebbinge et al. (1982), Alisauskas and Ankney (1992b), Alisauskas (2002)
	W N American arctic	California, Mexico	3–5 days	Endo		Herb		Raveling (1978)

Table 2 (Contd.)

Taxon	Breeding area	Wintering area	Time between arrival at breeding sites and incubation	Source of nutrients for repro	Energy store during migration	Diet	Diet shift	Reference
	Wrangel Is, Russia	California, Mexico	10–20 days			Herb		Zacheis et al. (2001)
Greater snow goose *Anser c. atlanticus*	E high arctic Canada, NW Greenland	E USA	2 weeks	Endo and exo	Yes (fat)	Herb		Gauthier et al. (1984, 1992, 2003), Gauthier and Tardif (1991), Gauthier (1993), Choinière and Gauthier (1995), Giroux and Bergeron (1996)
Ross's goose *Anser rossii*	Central and E arctic Canada	SW USA, US and Mexican Gulf Coast	3–5 days	Endo	Yes	Herb		Raveling (1978), McLandress and Raveling (1981a, b)
Atlantic canada goose *Branta canadensis/ interior*	Quebec, Canada	Coastal E USA, New England–South Carolina	Some days to some weeks	Endo and exo	Yes	Herb		Bellrose (1978), McLandress and Raveling (1981a, b), Carrière et al. (1999)
North atlantic canada goose *B. c. interior*	Newfoundland, Labrador, W Greenland	Coastal E USA	Some days to some weeks	Endo	Yes	Herb		Bellrose (1978), McLandress and Raveling (1981a, b)
Canada goose *B. c. interior*	N Ontario W of James Bay and S of Hudson Bay	Wisconsin and Illinois	5–6 weeks	Endo	Yes	Herb		Gates et al. (2001)
Canada goose *B. c. hutchinsii/parvipes*	Arctic Canada–Baffin Is to Queen Maud Gulf S to Hudson Bay	Oklahoma, Texas and New Mexico		Endo		Herb		Croft (1999) in Alisauskas (2002)
	Victoria Island and Queen Maud Gulf S to N Alberta	SE Colorado, NE New Mexico, Oklahoma and Texas		Endo		Herb		Croft (1999) in Alisauskas (2002)
Dusky canada goose *B. c. occidentalis*	Copper River Delta, Alaska	Willamette and Colombia river valleys, Oregon and Washington	2 weeks	Exo		Herb		Bromley (1984) in Budeau et al. (1991), Bromley and Jarvis 1993
Cackling canada goose *B. c. minima*	Yukon-Kuskokwim Delta, Alaska	W Oregon, W Washington	10–20 days	Exo	Yes	Herb		McLandress and Raveling (1981a, b), Zacheis et al. 2001
Taverner canada goose *B. c. taverneri/ parvipes*	Interior Alaska	Washington to California				Herb		Zacheis et al. (2001)
Giant canada goose *B. c. maxima*	Canada between lakes Winnipeg and Manitoba	Mississippi flyway: Minnesota		Endo and exo	Prior to migration	Herb		McLandress and Raveling (1981a, b), Thomas (1983)
Barnacle goose *B. leucopsis*	East Greenland	NW Scotland, Ireland			Yes	Herb		Ogilvie et al. (1999)

Table 2 (Contd.)

Taxon	Breeding area	Wintering area	Time between arrival at breeding sites and incubation	Source of nutrients for repro	Energy store during migration	Diet	Diet shift	Reference
	Svalbard	SW Scotland	12 days	Endo	Yes	Herb		Pettifor et al. (2000), Cope (2003), Prop et al. (2003)
N Russia, E Baltic	N Germany, Netherlands	Some days	Endo	Yes	Herb		Ganter et al. (1999)	
Dark-bellied brent goose *B. bernicla bernicla*	W Siberia	Coastal W Europe	3–5 days	Exo	Yes	Herb	Yes	Ebbinge et al. (1982), Teunissen et al. (1985), Prop and Deerenberg (1991), Drent (1996), Pettifor et al. (2000), Van der Wal et al. (2000)
Light-bellied brent goose *B. b. hrota*	Svalbard, N Greenland	Coastal Denmark, NE UK	< 2 weeks	Endo and exo	Yes	Herb	Yes	Ankney (1984), Clausen et al. (1999), Van der Wal et al. (2000), Clausen et al. (2003)
	E Canadian high arctic	Coastal Ireland	2 weeks	Endo and exo	Yes	Herb		Merne et al. 1999
Wood duck *Aix sponsa*	E North America, W Cuba	Partial migrant S to Mexico	Some weeks	Exo		Gran/omni	Yes	Coulter (1955), Bellrose (1978), Dugger and Frederickson (1992), Jeske (1996)
Eurasian wigeon *A. penelope*	W Siberia and NW, NE Europe	NW Europe		Exo		Herb/omni	Yes	Jacobsen 1989
American wigeon *A.. americana*	NW to Central E N America	N American Atlantic and Pacific coasts, C America, Caribbean	1–2 weeks	Exo	Yes	Herb	Yes	Bellrose (1978), Jacobsen (1989), Jeske (1996)
Gadwall *A. strepera*	S Canada and Alaska, N USA	S and W N America, Mexico	3–4 weeks	Endo and exo		Herb/omni	Yes	Dwyer (1975), Paulus (1984), Ringelman (1990), Ankney and Alisauskas (1991), Jeske (1996)
Common teal *A. .crecca*	N and NW Europe	NW Europe	Some weeks	Endo		Gran/omni	Yes	
Green-winged teal *A. carolinensis*	Alaska, Canada, NW USA	USA, Mexico, Caribbean	Some weeks	Exo	Yes	Gran/carni	Yes	Coulter (1955), Bellrose (1978), DeRoia and Bookhout (1989), Jeske (1996)
Mallard *A. platyrhynchos*	N Europe	NW Europe E to the Baltic	Some days	Endo and exo	Yes	Gran/omni		Asplund (1981), Robinson et al. (2003)

Table 2 (Contd.)

Taxon	Breeding area	Wintering area	Time between arrival at breeding sites and incubation	Source of nutrients for repro	Energy store during migration	Diet	Diet shift	Reference
Alaska, Canada, USA	SW and S Canada, USA	Some days	Endo and exo	Yes	Gran		Bellrose (1978), Krapu (1981),	Gruenhagen and Fredrickson (1990), Owen and Black (1990), Jeske (1996), Dugger (1997)
American black duck *A. rubripes*	E Canada, NE USA	E USA	<2 weeks	Endo and exo	Yes	Herb/omni		Coulter (1955), Bellrose (1978), Owen and Reinecke (1979), Jeske (1996), Longcore et al. (2000)
	Central Canada, N USA	Mississippi flyway	9 days to 3 weeks	Endo and exo	Yes	Herb/omni	Yes	Bellrose (1978), Owen and Reinecke (1979), Barboza and Jorde (2002)
Northern pintail *A. acuta*	Alaska, Canada, N USA	SW Canada, USA, Mexico, Caribbean, C America	Some days	Endo		Gran/omni		Jeske (1996), Fredrickson and Heitmeyer (1991)
Blue-winged teal *A. discors*	N America	S USA, C America, N S America	Some days	Endo and exo	Yes	Gran/omni	Yes	Taylor (1978), DeRoia and Bookhout (1989), Gammonley and Fredrickson (1995), Jeske (1996)
Cinnamon teal *A. cyanoptera*	W Central N America to NW Mexico	SW USA, Mexico, Central America	Some weeks	Exo		Gran/omni	Yes	Bellrose (1978), Thorn and Zwank (1993), Gammonley (1995)
Northern shoveler *A. clypeata*	Alaska, Canada, N USA	SW Canada, USA, Mexico, Central America	3 weeks	Exo* and endo**	Yes	Omni	Yes	Afton (1979)*, Ankney and Afton (1988)**, Ankney et al. (1991), DuBowy (1996), Jeske (1996), MacCluskie and Sedinger (2000)
Canvasback *A. valisineria*	Alaska, W Canada, NW USA	S USA, N Mexico	Some days			Herb		Bellrose (1978), Jeske (1996)
Redhead *A americana*	Alaska, W and S Canada, W USA	W, S and SE USA, Mexico	1 month	Exo		Herb/omni	Yes	Bellrose (1978), Jeske (1996), Custer (1993)
Ring-necked duck *A. collaris*	Central Alaska, Central and E Canada, Central and W USA	W, S and SE USA, Mexico	Some weeks	Endo		Gran		Owen and Black (1990), Alisauskas et al. (1990)
Lesser scaup *A. affinis*	N America, Central America	N America, Central America	3 weeks	Endo and exo	Yes	Carn		Bellrose (1978), Gammonley and Heitmeyer (1990), Ankney et al. (1991), Jeske (1996), Anteau and Afton (2004)

Table 2 (Contd.)

Taxon	Breeding area	Wintering area	Time between arrival at breeding sites and incubation	Source of nutrients for repro	Energy store during migration	Diet	Diet shift	Reference
Common eider *Somateria mollissima borealis*	Arctic NE Canada	Atlantic coast Canada and SW Greenland		Endo		Carn		Owen and Black (1990)
	Atlantic NE Canada	Atlantic Coast, Canada, N USA		Endo		Carn		Owen and Black (1990)
Steller's eider *P. stelleri*	N Siberian coast, N and W Alaska	SW Alaska, Aleutians, Kamchatka, Kuril Is	Some weeks	Exo		Carn		Fredrickson (2001)
Harlequin duck *Histrionicus histrionicus*	E Canada, W and SE Greenland	Coastal NE Canada and USA, E and SW Greenland		Exo		Carn		Rodway (1998)
Barrow's goldeneye *Bucephala islandica*	N Iceland	Iceland		Exo	Yes	Carn		Savard (1988)

agricultural habitats that nutrient reserve deposition was neither time- nor resource-limited during spring migration. Consequently, changes in agricultural practices may have great influence on population dynamics of geese, and potentially other Anatidae.

Some geese and swans actually accumulate reserves at spring staging sites (e.g. pink-footed goose, Madsen 1985; greater snow goose *A. caerulescens atlantica*, Gauthier et al. 1992; Giroux and Bergeron 1996; trumpeter swan *C. buccinator*, LaMontagne et al. 2001; Table 2). Again, this supports the idea that staging areas may be important for the build-up of body reserves, and that the former indirectly influence breeding success (LaMontagne et al. 2001). Klaassen (2002) pointed out the crucial role of body size for refuelling needs: smaller species can carry smaller stores, and therefore they depend more on high-quality foraging sites along the flyway. Differences in storage capacity may also partly explain differences between species in energy and nutrient requirements for body maintenance after arrival on the breeding grounds, for egg production, as well as for the tendency to defend a territory.

In order to manage spring staging areas efficiently we recognize the importance of understanding food and habitat availability at these sites, and the same goes for habitat and food selection processes in the birds (e.g., Markkola et al. 2003; Arzel and Elmberg 2004).

Social interactions and competition

Most geese arrive at their breeding sites when there is still snow on the ground, i.e. at a time of low food supply. Moreover, they often have a migratory timetable such that they travel with the progression of snowmelt, having to make successive habitat and diet choices at several sites (Hupp et al. 2001). Under such circumstances, the social status of individuals may strongly affect feeding success. In particular, paired females preparing for breeding may enjoy priority to food sources by means of vigilant males (e.g., greenland white-fronted goose *A. albifrons frontalis*, Fox and Madsen 1981).

Paired male dabbling ducks also guard their female during winter and migration, so that the latter can feed more efficiently to meet pre-breeding nutritional requirements (McKinney 1986; Guillemain et al. 2003). Hepp (1984) proposed that social factors during the non-breeding period may lead to delayed nesting and reduced clutch size in first-year breeding ducks. Indeed, irrespective of sex paired ducks have a higher dominance rank than unpaired ones, again frequently giving better access to food resources (Guillemain et al. 2003). Finally, temporary on-site territoriality during spring migration may also increase the chances of enjoying an unshared and undisturbed feeding area (Seymour 1974; Savard 1988).

If and when it occurs, competition for food may involve not only other Anatidae, but any other organism feeding on invertebrates or seeds at stopover sites. One documented case from wetlands used by staging as well as breeding ducks concerns salamanders (Benoy et al. 2002), but the possible role of competition with fish and other animals in spring remains virtually unexplored. This is definitely a priority for future research. Thus, many aspects of local ecosystems need to be addressed in order to get a comprehensive picture of the quality of spring habitats and to understand potentially limiting factors. We here also see a neglected interface between community ecology and population processes, even if the scope is restricted to waterfowl (cf. Nudds 1992).

Waterfowl studies addressing density dependence have been carried out on breeding as well as on wintering grounds, but never at spring staging areas. Spring is undoubtedly 'a lean time' of the year, making it reasonable to assume that some type of limitation may occur at times, and consequently that density dependence is rather more likely to operate than in other seasons. We think that management as well as ecological theory may benefit from studies addressing density dependence in spring, preferably those encompassing several stopover areas intensively used by waterfowl. Buffer effects (Zwarts 1976; Gill et al. 2001; Newton 2004), in particular, would be interesting to study, as such density-dependent processes may influence survival and breeding success at larger scales, possibly also population regulation.

Energetics

Migration is a costly activity per se (see references above), and exogenous resources seem to be essential to almost all Anatidae during migration (e.g., dusky canada goose *B. canadensis occidentalis*, Bromley and Jarvis 1993; brant *B. bernicla nigricans*, Vangilder et al. 1986). Fat gain prior to and during migration increases a bird's maximum flight range (Odum et al. 1961; Pennycuick 1975; Wypkema and Ankney 1979). Deposition prior to migration is made possible partly by increasing food assimilation efficiency, partly by reducing energy use for normal activities, but principally by increasing food intake, also called hyperphagia (e.g., Madsen 1985; Gauthier et al. 1992; McLandress and Raveling 1981a). For example, the latter authors state that ''hyperphagia and the associated accumulation of body reserves occurred less than one month prior to departure for the breeding grounds, also coinciding with the highest level of protein in new growth grass''.

Onw way of avoiding starvation when arriving at the breeding grounds is to depart for migration as soon as the maximum fat quantity has been accumulated (barnacle goose, Prop et al. 2003), and use it on the breeding ground to meet subsequent breeding requirements (ring-necked duck *Aythya collaris*, Hohman et al. 1988; barnacle goose, Prop et al. 2003).

Given the information above, it is fair to ask whether fatter birds in general are better migrants and also more successful breeders. However, fat is not always beneficial to carry; it may increase predation risk by reducing manoeuvrability and the ability to take off quickly (Lima 1986; Witter and Cuthill 1993). LaGrange and Dinsmore (1988) stressed the somewhat contradictory pattern that maintenance and gain of body weight and lipids occur in paired female mallard during spring migration, a period of the annual cycle when they incur a variety of energetic costs, including migratory flight, thermoregulation and gonadal growth.

It is often said that survival and reproduction of northern Anatidae are potentially affected by body condition during the non-breeding season (Heitmeyer 1988; Hohman et al. 1988; Gammonley and Heitmeyer 1990; Ebbinge and Spaans 1995; Tamisier and Dehorter 1999; Barboza and Jorde 2002). If and when such a connection occurs, it may also lead to carry-over effects between years. Long-term fluctuations in body condition are sometimes related to population trends, as shown by Anteau and Afton (2004) in lesser scaup *A. affinis*.

In contrast to the geese, there are very few studies of nutrient reserves in ducks in spring, especially of their importance to subsequent reproductive success (but see mallard, Krapu 1981; northern pintail *A. acuta*, Esler and Grand 1994; black duck *A. rubripes*, Barboza and Jorde 2002).

Spring migration and breeding success

Abundant food supply in spring is often supposed to increase breeding success (Teunissen et al. 1985; Ebbinge and Spaans 1995), but in the literature there are diverging opinions about the importance of food abundance at the arrival at breeding grounds. As underlined by Carrière et al. (1999), food availability was traditionally thought to be so low in spring in the arctic that female geese were not always capable of meeting the energy requirements for both daily maintenance and egg-laying. However, these authors clearly demonstrated that food availability increased dramatically right after snow-melt, providing suitable foraging conditions to the geese. Other studies show that females increase their body mass before or during egg production (Wypkema and Ankney 1979; Budeau et al. 1991; Bromley and Jarvis 1993; Choinière and Gauthier 1995; Ebbinge and Spaans 1995), indicating that energy intake provided at least slightly more than just the requirements for daily maintenance (Ganter and Cooke 1996).

Despite generally being seen as capital breeders, in some geese most of the energy necessary for egg formation and incubation comes from food eaten on the breeding grounds (greater white-fronted goose *A. albifrons frontalis*, Budeau et al. 1991; dusky canada goose, Bromley and Jarvis 1993; greater snow geese, Choinière and Gauthier 1995).

Intermediate scenarios, i.e. when birds rely on exogenous as well as endogenous resources, may occur when the time available for feeding between arrival at breeding grounds and egg-laying varies considerably among females and/or among years within populations (Raveling 1978). Variation in the timing of nesting can in some cases be related to variation in food availability prior to egg formation (Prop and DeVries 1993). We conclude that food availability and use in the arctic in spring may indeed be of primary importance to breeding success. Gardarsson and Einarsson (1994) implied that there is a causal link between pre-breeding abundance of invertebrate food at the breeding site and subsequent local production of young in dabbling ducks.

Based on current knowledge, we argue that there is a general need to adopt a flyway perspective when studying the relative importance of stopover areas for accumulation of body reserves. To some extent, female waterfowl use endogenous reserves (both lipids and proteins) for clutch formation, but in addition they may use exogenous resources, especially to meet protein requirements (Alisaukas and Ankney 1992a).

Different strategies exist among geese (Klaassen 2002), though, as some species breed right after arrival at the breeding grounds (e.g. dark-bellied brent goose *B. bernicla bernicla*), whereas others forage for some weeks before initiating egg-laying (Carrière et al. 1999; greater white-fronted geese, Budeau et al. 1991; black brant *B. bernicla nigricans*, Raveling 1978; Lindberg et al. 1997). How much females rely on body reserves for egg formation, in other words to which degree they are income or capital breeders, may also vary within populations. Still, most geese begin egg-laying within 2 weeks after arrival at the breeding grounds. Egg-laying thus generally takes place when food is still scarce, but pre-nesting feeding has received little attention in the literature. The few published studies agree that exogenous resources at breeding grounds prior to laying seem to be crucial (Budeau et al. 1991; Ganter and Cooke 1996), although they may be in short supply (Bromley and Jarvis 1993; Fox 2003). Acquiring the full range of different nutrients is so crucial that, in Alaska, several goose species forage on clam shells in spring, supposedly to meet calcium requirements (Flint et al. 1998). Clutch size is influenced by feeding activities and nutrient storage, especially during the late stage of the migration and sometimes also after the arrival at breeding grounds (cf. LaMontagne et al. 2003): later spring migrants such as black brant have a larger clutch than early migrants, a difference supposed to be due to prolonged access to spring foraging habitats in the former species (Lindberg et al. 1997).

The degree to which birds rely on body reserves depends not only on body size, but also on the distance from the last stopover sites to the breeding area (Klaassen 2002; pink-footed goose, Drent et al. 2003). Many studies suggest that breeding strategies of waterfowl are generally flexible, and that this may be an evolutionarily valuable response to variability in food resources or other external factors (Madsen 2001).

Nutrient storage at spring stopovers and its impact on subsequent reproduction have been studied in very few ducks (e.g., ruddy duck *Oxyura jamaicensis rubida*, Alisauskas and Ankney 1994). This is indeed a shortcoming, since small species are supposed to be mainly income breeders, thus being more sensitive to changes and variations in food availability during and after spring migration. We see an imminent need for more research addressing how habitat use, food quality, and food quantity along spring migration routes are related to subsequent breeding success. This is not only a scientific priority, as spring staging sites are underrepresented in the international network of protected wetlands.

Related to this, we see a great value of developing a model for the initiation time of egg formation in ducks (for geese, see Ganter and Cooke 1996). Such a tool would allow assessment of when nest initiation date and clutch size are determined, hence also indicating which is the most crucial part of the pre-nesting migration. Some ducks indeed start laying eggs just after arrival on the breeding grounds, especially at high latitudes (blue-winged teal *A. discors*, Gammonley and Fredrickson 1995; northern pintail, Fredrickson and Heitmeyer 1991; steller's eider, Fredrickson 2001). There may also be a very general advantage of nesting early (Krapu 1981; Elmberg et al. 2005). We argue that food availability and nutrients stored at spring stopovers can be assumed to be of primary importance to ducks, not only for body maintenance and survival, but also for subsequent breeding success. A better knowledge of their spring ecology will help to determine when and where food, habitat availability and suitability affect fecundity the most, thereby helping to devise the most appropriate and efficient management and conservation measures.

Conclusions

Although the ecology of long-distance migrating swans, geese, and ducks (Anatidae) in the holarctic has been studied extensively on breeding and wintering grounds, comparatively little information is available about spring migration and the first weeks on the breeding grounds. In the literature that does exist, geese are much over-represented, especially studies of staging and breeding arctic species.

Despite the general paucity of springtime studies of waterfowl, there are some unquestionable general patterns. Most species make a long and energetically costly migratory journey at a time of year when energy-rich food items are often still scarce. Breeding is costly, too, often starting soon after arrival at the breeding grounds. For geese, there is fairly consistent evidence for a general causal link between habitat quality at staging sites, energy accumulation, and subsequent breeding success. A similar connection may exist in ducks, but there is as yet very little evidence for this.

The main result of this review is that there is surprisingly little information about the springtime ecology of small to medium-sized waterfowl. We have identified many research needs, of which some of the more pressing are: (1) understanding to what extent different species are 'income' versus 'capital' breeders, specifically which part of the pre-breeding period is most crucial to breeding success; (2) changes in time use, microhabitat use, and diet through spring; (3) food limitation, community composition and competition on staging sites; (4) the effect of disturbance on energy accumulation and breeding success; and (5) studies in general with a diel, circum-annual or pan-flyway perspective. These are not exclusively scientific issues, as migration and staging sites used in spring are still underrepresented in conservation networks, and probably also frequently managed in a suboptimal way.

Zusammenfassung

Ökologie von Anatiden beim Frühjahrszug: eine Übersicht

Der Frühjahrszug gilt als eine der kritischsten Phasen eines Jahres, insbesondere wegen seines Einflusses auf das nachfolgende Brutgeschäft. Eine Auswertung der vorhandenen Literatur zu Enten, Gänsen und Schwänen zeigt, dass, mit Ausnahme einiger Gänsearten, zur Ökologie von Wasservögeln beim Frühjahrszug nur recht wenig bekannt ist. Frühere Studien beschränkten sich vornehmlich auf die Frage nach der Aufnahme von Nährstoffen. Zu Rasthabitaten, zeitlichen Faktoren, Mikrohabitatwahl, Ernährungsverhalten, Verfügbarkeit von Nahrung, Nahrungsengpässe, Nahrungswahl, oder interspezifische Beziehungen ist nur echt wenig publiziert. Neben der Zusammenfassung des derzeitigen Kenntnisstandes ist es ein Ziel dieser Arbeit, Wissenslücken aufzudecken und Themenbereiche für zukünftige Forschungen aufzuzeigen.

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