Spring migration of waterfowl in the northern hemisphere: a conservation perspective

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Abstract

Spring migration is a key part of the annual cycle for waterfowl populations in the northern hemisphere, due to its temporal proximity to the breeding season and because resources may be limited at one or more staging sites. Research based on field observations during spring lags behind other periods of the year, despite the potential for fitness consequences through diminished survival or cross-seasonal effects of conditions experienced during migration. Consequently, conservation strategies for waterfowl on spring migration are often only refined versions of practices used during autumn and winter. Here we discuss the current state of knowledge of habitat requirements for waterfowl at their spring migratory sites and the intrinsic and extrinsic factors that lead to variability in those requirements. The provision of plant foods has become the main conservation strategy during spring because of the birds' energy requirements at this time, not only to fuel migration but to facilitate early clutch formation on arrival at the breeding grounds. Although energy sources are important to migrants, there is little evidence on the extent to which the availability of carbohydrate-based food is limiting for many migratory waterfowl populations.

Such limitation is relatively unlikely among populations that exploit agricultural grain during migration (*e.g.* arctic-nesting geese), suggesting that conservation strategies for these populations may be misplaced. In general, however, we found few cases in which an ecological understanding of spring-migrating waterfowl was sufficient to indicate true resource limitation during migration, and still fewer cases where conservation efforts ameliorated these limitations. We propose a framework that aims to address knowledge gaps and apply empirical research results to conservation strategies based on documented limitations and associated fitness impacts on migrating waterfowl. Such a strategy would improve allocation of scarce conservation resources during spring migration and greatly improve ecological understanding of migratory waterfowl and their habitats in the northern hemisphere.

Key words: conservation, limitations, lipids, nutrients, spring migration, waterfowl.

Spring is a critical phase of the annual cycles of waterfowl *Anatidae* sp. in the northern hemisphere because of the physiological and environmental conditions encountered during migration, and the co-occurrence of pre-breeding life-history events. Maintenance or acquisition of nutrient reserves at staging areas is generally necessary in order to complete migration, and is often also a prerequisite for successful breeding (Ankney *et al.* 1991; Jenni & Jenni-Eirmann 1998). Individuals often experience diminished food availability as they await the thaw of wetland habitats or because of food depletion by autumn-migrating birds (Stafford *et al.* 2006; Greer *et al.* 2009; Straub *et al.* 2012). Moreover, in addition to migration, many species are undertaking energetically expensive activities such as courtship, pair-bond maintenance and moulting into breeding plumage at this time (Heitmeyer 1988; Lovvorn & Barzen 1988; Richardson & Kaminski 1992; Hohman *et al.* 1997; Barras *et al.* 2001; Anteau *et al.* 2011a). Adverse and unpredictable weather can kill birds directly or lead to starvation by making food resources temporarily unavailable (Trautman *et al.* 1939; Newton 2006, 2007). Further, migratory movements themselves can be dangerous and energetically costly, requiring individuals and flocks to exploit habitats and foods that promote survival (*sensu* Fretwell 1972; Kaminski & Elmberg 2014). The choice of migratory strategy therefore represents important trade-offs with lasting consequences for individual fitness and population dynamics, which may be sensitive to management strategies used by conservation organisations along migratory corridors in the northern hemisphere.

Habitat conditions encountered during spring migration also have potential to influence waterfowl populations through cross-seasonal (or carry-over) impacts on individual reproduction (Davis *et al.* 2014, Sedinger & Alisauskas 2014). The seminal works of Weller (1975), Fredrickson and Drobney (1977), Ankney and MacInnes (1978), and others (*e.g.* Heitmeyer & Fredrickson 1981; Kaminski & Gluesing 1987) prompted research on the nature and mechanisms for cross-seasonal effects on

waterfowl in particular and migratory birds in general (Drent & Daan 1980; Harrison *et al.* 2011; Sedinger & Alisauskas 2014). This work has shown evidence for various cross-seasonal relationships in waterfowl, for populations both in Europe and in North America, and ranging across species from those using capital breeding strategies (*e.g.* Lesser Snow Goose *Chen c. caerulescens*; Alisauskas 2002) to those which mainly acquire the food resources needed for egg-laying on or near the breeding territories ("income breeders"; *e.g.* Eurasian Teal *Anas crecca crecca*; Guillemain *et al.* 2008). Although spring migration is widely recognised as being an important time both for individual survival and for subsequent breeding success, it remains largely understudied in comparison with other stages in the annual cycle (Arzel *et al.* 2006), and management strategies during this period are often refinements of practices intended for breeding or wintering populations (Soulierre *et al.* 2007).

In this paper we synthesise published information on the habitat requirements of waterfowl during spring migration and discuss potential applications of the knowledge for conservation initiatives at migratory stopover areas. Arzel *et al.* (2006) has made a comprehensive review of the current state of literature on spring-migrating waterfowl, so we do not intend to repeat their work here. Rather, we endeavour to assess available information and consider gaps in knowledge that have the potential to diminish the efficacy of conservation strategies aimed at enhancing habitat conditions for waterfowl on spring migration. Identifying knowledge gaps can inform the management and conservation

of waterfowl at spring staging areas and help to set research priorities for improving our understanding of migratory species. Specifically, our objectives are to: 1) review the general requirements of waterfowl on spring migration and discuss intrinsic and extrinsic factors that influence these requirements, 2) discuss inter-specific differences in the requirements of migrating waterfowl and the limitations imposed by habitat conditions encountered during spring, and 3) propose a framework for evaluating limitations on waterfowl during spring migration, and for implementing habitat management and conservation that may alleviate or mitigate these limitations.

General requirements of spring-migrating waterfowl

Body reserves which can be converted into metabolic energy are the most recognised currency for avian migration (Jenni & Jenni-Eirmann 1998) and are also necessary for subsequent reproduction in many waterfowl species (Ankney *et al.* 1991). Lipids provide the most efficient means of storing energy for migration, and lipid metabolism therefore is considered a key factor influencing onwards migration and the selection of stopover sites. Individuals are expected to choose habitats where energy sources are readily available during migration and avoid energetically expensive staging areas (Bauer *et al.* 2008; Mini & Black 2009; Brasher 2010). Waterfowl gain energy and build lipid reserves from seeds, other plant material and invertebrates, with the relative contribution of each to the diet varying considerably among species. Similarly, the relative distribution of plant

and invertebrate foods varies across different foraging habitats, which has species-specific implications for food availability at each site (Straub *et al.* 2012). Many North American species use abundant waste agricultural seeds in croplands as a carbohydrate source during spring migration (Krapu *et al.* 1995; Anteau *et al.* 2011b, Pearse *et al.* 2011). Others rely on invertebrates to build lipid reserves, which are likely to be more variable in abundance and distribution, and also are apparently declining in some regions (Anderson 1959; Wilson *et al.* 1995; Anteau & Afton 2008a,b; Anteau *et al.* 2011c; Straub *et al.* 2012).

Nutrients other than lipids are also required by waterfowl during spring, most notably protein, essential amino acids and minerals (*e.g.* calcium). Evidence from Snow Geese suggests that some waterfowl mobilise protein reserves gained during migration for subsequent reproduction (Ankney & MacInnes 1978; Gauthier *et al.* 2003). Moreover, moulting birds require protein to synthesise feather tissue (Heitmeyer 1988; Barras *et al.* 2001); some species consume protein-rich foods during contour feather moult (Fox *et al.* 1998; Anderson *et al.* 2000; Anteau *et al.* 2011a), whereas protein reserves may be related to contour feather moult intensity in other species (Lovvorn & Barzen 1988). Protein is also required for repairing muscles injured or catabolised during flight, similar to the way in which fat reserves are consumed and replenished during migration (Guglielmo *et al.* 2001; Piersma 2002). Earlier work has established the importance of a diverse diet for maintaining body condition during winter (Loesch & Kaminski 1989),

suggesting that foraging decisions may be influenced by the specific amino acids to be found in food items (Heitmeyer 1988). However, our understanding of the role of specific nutrients (particularly at the essential amino acids and fatty acids level) for maintaining body condition at different times of year is still in its infancy.

The most basic requirement for all waterfowl (and indeed for most living organisms) is water. Water is gained primarily by drinking, but it can also be acquired in the diet or derived through metabolic pathways. Wetlands provide not only a water source but are important for a range of functions most notably foraging, roosting, pair formation (Anderson & Titman 1992), safety from predators, isolation from disturbance and protection from inclement weather conditions (LaGrange & Dinsmore 1989; Havera *et al.* 1992; Zimmer *et al.* 2010). Research in Europe revealed that many geese migrate toward breeding areas through agricultural regions, but that bird distributions may be constrained within a radius of a safe body of water or ice that can function as a predator-free overnight roost (*e.g.* the spring migration of Pink-footed Geese *Anser brachyrhynchus* within Britain is thus confined to particular areas; Bell 1988; Fox *et al.* 1994). Similar patterns have been shown with migrating Mallard *Anas platyrhynchos* (LaGrange & Dinsmore 1989) and geese (Anteau *et al.* 2011b) in agricultural landscapes in central North America.

Factors influencing waterfowl requirements during spring migration

Although these are generally universal for waterfowl during spring migration,

the relative importance of each varies within and among species in response to conditions encountered *en route* (*e.g.* weather, disturbance) and in accordance with their migration and/or breeding strategies. Weather can influence individual requirements during migration, particularly among early migrants that may encounter physiologically demanding conditions on reaching high latitudes before the ice and snow has melted in the northern part of their range. For example, LaMontagne *et al.* (2001) reported differences in foraging activity among spring-migrating Trumpeter Swans *Cygnus buccinator* in response to cold temperatures encountered during migration. It is likely that early migrants exposed to wide variations in temperature and precipitation during spring would exhibit similar weather-dependent foraging and roosting behaviours, such as hyperphagia or seeking thermal cover. Weather affects habitat conditions along the migration route, and generally influences the availability of food and other resources throughout the year, as discussed further below.

Disturbance is another important factor influencing the relative importance of habitat requirements for migrating waterfowl (Madsen 1995), as it may affect the timing of migration strategies or individual body condition during stopover (Drent *et al.* 2003; Feret *et al.* 2003; Pearse *et al.* 2012). Variation in predation pressure during spring migration also may influence foraging ecology or the ability to exploit resources necessary for migration (Guillemain *et al.* 2007).

Variation in breeding and migration strategies leads to considerable variation in the conditions required by waterfowl throughout migration. Birds expected to adhere primarily to a capital breeding strategy (*e.g.* arctic nesting geese) need more resources from stopover locations than those using an income-breeding or local-capital strategy (*sensu* Klaassen *et al.* 2006), in which they acquire most breeding resources and nutrients from breeding habitats. Variation in migration strategies among species invoking an income-breeding strategy further differentiates requirements throughout migration. Income migrant waterfowl (*e.g.* Eurasian Teal; Arzel *et al.* 2007) rely especially on lipids acquired at staging sites to fuel subsequent flights, whereas other species may carry reserves to facilitate onward migratory movement (Krapu *et al.* 1995; Pearse *et al.* 2011). Across this gradient, from capital breeding species to income migrants, considerable variation in nutrient accumulation and storage rates have been documented throughout spring migration. For example, Garganey *Anas querquedula* in southern France effectively forgo nutrient reserve accumulation during stopover (Guillemain *et al.* 2004), whereas Greater White-fronted Geese *Anser albifrons* in the Rainwater Basin of Nebraska accumulate 11–22 g (dry) mass/day in the staging areas (Krapu *et al.* 1995).

European geese provide an example of variable requirements during migration that manifest as a result of variable migration strategies. These populations rely upon the new growth of grasses and sedges at higher latitudes following the emergence of the "green wave" of above-ground production following spring thaw (Drent *et al.* 1978; van

der Graaf *et al.* 2006; van Wijk *et al.* 2012). Tracking this green wave is more easily undertaken in a series of relatively short flights, as is the case of Greater White-fronted Geese *Anser albifrons* in continental Europe. In contrast, Greenland White-fronted Geese *A. a. flavirostris* make long overseas flights from Britain and Ireland to staging areas in Iceland, and from there to breeding areas in west Greenland (Fox *et al.* 2003). Such stepping-stone migrants have to take calculated risks when moving onwards to staging areas, perhaps without adequate cues to predict meteorological conditions and the advancement of spring phenology further ahead (Fox *et al.* 2006; Tombre *et al.* 2008). Variation in the availability of spring staging areas has considerable effects on nutrient acquisition strategies adopted by the species with the same or similar body structure but in different parts of its range. The Greenland White-fronted Goose may deplete 800–900 g of fat when flying from winter quarters to spring staging areas in Iceland, and there it must acquire similar fat stores for the onward journey to breeding areas in west Greenland (Fox *et al.* 2003). Remarkably, the Greenland population now leaves the wintering areas on average three weeks earlier than 25 years ago (Fox & Walsh 2012), but because of a lack of warmer springs in Greenland it remains longer in Iceland (Fox *et al.* 2012) and fattens at a slower rate to arrive on the breeding areas at the same time as recorded in the 1860s (Fox *et al.* 2014). Such behaviour suggests considerable phenotypic plasticity in migration behaviour and ability to acquire fat stores in a fluctuating environment.

Distinguishing between requirements and limitations during spring migration

There is considerable variation between waterfowl of the northern hemisphere in the conditions that best match their social, ecological and physiological requirements at different stages of migration, creating many challenges for research and conservation along the flyway. However, in many cases the populations' requirements are met through large-scale habitat use and selection processes (*i.e.* adherence to flyways with necessary resources). For example, no studies of mid-continent goose populations in North America have documented nutrient deficiencies during migration or upon arrival on the breeding grounds, despite the importance of nutrient reserves to these populations having been established. In this case, adherence to the central flyway, where the availability of waste agricultural seed exceeds population needs, ensures nutrient accumulation and maintenance during migration and increases the likelihood of successful reproduction. Thus, although energy is the most important nutritional requirement among these migrating geese during spring, its availability (at least in the form of carbohydrates derived from agricultural seeds) is not a limiting factor during migration (Krapu *et al.* 1995; Jefferies *et al.* 2004; Stafford *et al.* 2006; Foster *et al.* 2010; Anteau *et al.* 2011b). This example raises the need for a distinction between requirements (resources that sustain migration and subsequent breeding) and limitations (resources that are not provided in sufficient supply to meet fully the needs of

individuals at the time and/or thereafter) for spring migrating populations, which in turn should guide current and future conservation strategies developed for these populations. Such a distinction is fundamental for the effective implementation of conservation throughout the annual cycle, but is not yet explicitly recognised in conservation strategies for spring-migrating waterfowl. This is likely due to the uncertainty surrounding mechanisms regulating populations during the period and the aforementioned tendency to adapt wintering conservation strategies (*e.g.* provision of energy) for spring-migrating waterfowl. Misguided conservation strategies based only on requirements, rather than a limiting resource, may lead to ineffective conservation.

In populations where the availability of a necessary resource is limiting, observations of habitat use and distribution patterns for the birds during migration are likely to describe these limitation(s), which may be driving cross-seasonal effects on population productivity. The opposite is also likely; when resources are not in limited supply, populations may be freed from constraints on production originating during spring migration (Jefferies *et al.* 2004). Limitations of waterfowl during migration vary spatially and temporally, and the scale at which limitations are assessed is important and should be determined by management objectives. For example, food depletions at local scales may or may not be consequential for waterfowl populations, but regionally depressed food resources from drought or other impacts could influence annual recruitment (*e.g.* Davies & Cooke 1983).

In the former case, management may be ineffective at improving population productivity through spring migration, whereas in the latter, large-scale efforts to abate food limitation would likely have population-level implications. Therefore, research during spring migration should seek to identify limitations at appropriate spatial scales, through intensive study of migrant habitat use and behaviour, so as to identify important limitations on populations. This knowledge can then be applied to the development and delivery of conservation strategies for spring-migrating waterfowl. Additionally, identification of habitat limitations during spring migration might be investigated and used cautiously and insightfully to reduce populations of burgeoning species, such as Lesser Snow Geese, whilst ensuring no impacts to other waterfowl species.

Evidence for habitat limitations in other periods of the annual cycle exists. Availability of suitable breeding habitat in the North American prairies is a well-documented driver of annual population dynamics for a range of waterfowl (Johnson & Grier 1988; Bethke & Nudds 1995; Reynolds *et al.* 2001), and population-level implications of food shortages on the wintering grounds has similarly been documented for various species (Heitmeyer & Fredrickson 1981; Kaminski & Gluesing 1987; Raveling & Heitmeyer 1989). However, few studies have been conducted at an appropriate spatial and temporal scale to document population-level limitations during spring. Here we highlight a case where research has been conducted at appropriate scales to document limitations

with the potential to inform conservation strategies for Lesser Scaup *Aythya affinis* on spring migration. Considerable research has been conducted on the ecology of the Lesser Scaup in spring following range-wide population declines throughout North America since the 1980s. We have therefore taken this body of work as an example of the benchmark necessary for achieving a reasonable understanding of populations-level limitations during migration, which may be applied to the conservation of other species during spring migration.

Research conducted along the Lesser Scaup's mid-continent spring migration corridors indicated that the females' lipid reserve levels had declined throughout the upper Midwest since the 1980s (Anteau & Afton 2004, 2009a), but not on wintering areas in the southern Mississippi Flyway (Anteau & Afton 2004; Vest *et al.* 2006). This work led to the spring-condition hypothesis, which predicted that females were unable to acquire energy or nutrients required during spring migration from stopover habitats through the Midwest. The limitation was predicted to result in decreased survival or diminished productivity from poor condition upon arrival in the breeding areas, reduced breeding propensity, delayed breeding or a combination of these (Anteau & Afton 2004, 2009a). Further research demonstrated that females were catabolising lipid reserves at spring migration stopover areas throughout the Midwest where they were expected to be storing lipids, lending support to the proposed link between habitat conditions during migration and diminished condition prior to the breeding season (Anteau & Afton 2011).

Research on wetlands used as stopovers during migration in the Midwest indicated that the availability of amphipods, an important, lipid-rich food item for migrating and pre-breeding Lesser Scaup (Arts *et al.* 1995; Lindeman & Clark 1999; Anteau & Afton 2009b), had declined in the region in conjunction with the documented declines in body condition (Anteau & Afton 2006, 2008a, b; Anteau *et al.* 2011c). Lesser Scaup select habitats with abundant amphipods (Lindeman & Clark 1999; Anteau & Afton 2009b); however, they likely use proximate cues (*e.g.* turbidity) to identify wetlands previously rich in amphipods, but which are now less numerous due to land use changes and invasions of fish into traditionally fish-free habitats (Anteau & Afton 2008a, 2009b). Spring is an energetically and nutritionally costly period for Lesser Scaup; thus, they clearly require both nutrient- and energy-rich foods. However, their adaptation to consuming an animal-based diet and the evidence reviewed above suggests that Lesser Scaup are likely limited by lipid availability during migration in the Midwest. Further research in the region suggested that amphipod abundance in stopover habitats may be subject to management (Anteau & Afton 2008a; Anteau *et al.* 2011c) and could focus on regions with high annual Lesser Scaup use in the Midwest (Anteau & Afton 2009b). Accordingly, implications of the research were to focus on identifying these key Lesser Scaup migration habitats in the region and to undertake work to improve the availability, quality and productivity of amphipods and other invertebrate food sources through wetland conservation

practices, such as the implementation of upland vegetation buffers and manipulating fish densities (Anteau *et al.* 2011c).

This example with Lesser Scaup illustrates the role of large-scale research on ecology and habitat use of migrating waterfowl, for identifying limitations and focusing management of those limitations at relevant scales, with a view to improving conditions encountered during migration. Large-scale relationships between population productivity and limitations encountered during spring migration are one case in which an explicit focus on limitations in conservation is appropriate. A similar focus has applications at finer spatio-temporal scales for improving local management efforts and the value of habitat reserves intended for use by spring migrants. For example, detailed studies of Lesser Snow Goose stopover ecology in the Rainwater Basin of central Nebraska has shown that fine-scale habitat features rather than energy requirements during migration drive the birds' use of space at staging sites (Pearse *et al.* 2010; Anteau *et al.* 2011c; Sherfy *et al.* 2011). Cornfields dominate the landscape in the Rainwater Basin, resulting in an estimated 10-fold net surplus of energy for Lesser Snow Geese and other migratory waterfowl (Bishop *et al.* 2008), but their location in relation to wetland roosts appears to be more important than variability between fields in the availability of waste grain. Changes in the distribution and area of wetlands therefore would likely have the greatest influence on space use by Lesser Snow Geese and other waterfowl in the region (Vrtiska & Sullivan 2009; Webb *et al.* 2010). Although the main nutritional requirements for spring-migrating Lesser Snow Geese are energy and protein, this example illustrates that the habitat factor most appropriate for management is the distribution of the primary limiting resource, wetlands.

Conclusions

Conservation planning during spring has traditionally focused on ensuring adequate food energy at stopover locations because of the well-established importance of energy during migration and the importance of lipid reserves for subsequent breeding (*cf.,* Ankney *et al.* 1991). For example, the North American Waterfowl Management Plan, through its Joint Ventures (*i.e.* public and private partnerships that plan and implement conservation activities), has typically adopted an approach of estimating the energetic carrying capacity (ECC) for a region based on estimated waterfowl population levels and goals during the non-breeding periods of the annual cycle. In this scenario, management activities during spring migration target provision of food resources to meet the energetic needs of waterfowl, typically through wetland creation, enhancement or management to produce carbohydrate-rich plant foods. The ECC approach relies on the critical assumption that energy derived from wetland habitats is the main requirement limiting waterfowl populations in spring. However, this assumption is largely untested for the spring migration period, and the importance of energy may not equate with limitation should food availability exceed the requirements of the population. We contend that the assumption that energy is

the primary limiting factor for waterfowl populations in spring may be untenable for many species that supplement their diet with residual agricultural food sources. Rather, any of the requirements of spring-migrating waterfowl discussed herein, or perhaps those yet undocumented, could limit spring migrants and have annual implications for survival or population productivity at various temporal and spatial scales.

In some cases, energy availability motivates habitat use and appears to limit population growth (*e.g.* the Lesser Scaup example described above). However, in other cases, energy during spring may not be limiting and can be in surplus (*e.g.* for mid-continent geese in North America). We suggest that the framework of ECC models could be reconsidered and perhaps restructured to evaluate whether energy is limiting for a species or guild within a conservation region. This would require a more comprehensive ECC that assumes that all sources of energy are equal if they are available to the species/group (*e.g.* agricultural *versus* wetland) and would require detailed information on the birds' diet and foraging behaviour given that all food sources – agricultural foods, wetland seeds and plants and invertebrates – must be considered as sources of energy. If careful evaluation indicates that available energy exceeds requirements for a given population or region, a focus on identifying or managing other possible limiting factors, if they exist, would be prudent. Such an approach may change the focus of conservation and management for some organisations (*e.g.* Joint Ventures, resource agencies); however, such an endeavour re-

focused on the ecology of relevant species would lead to more efficient allocation of resources and be more likely to affect measurable impacts to populations.

Habitat use and selection, along with diet and behavioural studies, can provide the foundation for determining what might be limiting a certain species at a certain staging area, if at all (Callicutt *et al.* 2011; Hagy & Kaminski 2012). Some studies of this nature to date have identified cross-seasonal effects related to spring limitations, but many questions remain and adoption of novel research will be necessary to resolve them. Telemetry and other spatially explicit individual-based studies and local-scale surveys of waterfowl concentrations would help identify factors associated with improved individual fitness in response to conditions experienced during spring and identify key habitats for foraging and roosting, respectively. Similarly, such studies may yield insights into the relative role of specific stopovers during migration and assist in prioritising further research and conservation across the expansive landscapes transited between wintering and breeding areas.

Many factors drive hierarchical resource selection and knowledge of these factors can inform conservation strategies (Johnson 1980). For example, intensive research on Sandhill Cranes *Grus canadensis* during spring migration at a major stopover area in central North America revealed that access to protein constituents of their diet was a strong driver of fine-scale habitat selection during staging, despite accounting for only *c.* 3% of their diet in the region (Krapu *et al.* 1984; Reinecke & Krapu 1986). This

research suggests that habitat selection and time investments among migrating waterbirds can be considerable in the acquisition of an apparently rare but important resource (*i.e.* a limiting resource). Similarly detailed studies for ducks and geese could assist in identifying other potential limiting factors.

Accomplishing a revised focus on limitations during spring conservation will require knowing the precise demands of the birds along the route of staging sites at different times during migration, and delivering the appropriate energy, protein, water and other resources such that birds may access them under a range of conditions (*e.g.* land use or climate change). Recognising the opportunities of expanded, individual-based cross-seasonal studies opens up a portfolio of research objectives that asks what birds need during spring, and how can we provide them most effectively, in a way that enhances condition, survival and preparation for the breeding season, regardless of species. The challenge for conservation will be to provide resources in adequate quantities to confer benefits to individuals of targeted populations and species. Such a task would be difficult given the dearth of information on factors truly limiting some waterfowl populations during spring. Nonetheless, until limiting factors are identified (or ruled out) it would be difficult to design and implement truly effective conservation programmes for populations of conservation concern.

Acknowledgements

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