# Habitat and resource use by waterfowl in the northern hemisphere in autumn and winter

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## Abstract

A particular aim of avian ecologists, especially those studying waterfowl *Anatidae*, in the 20th and early 21st centuries has been to elucidate how organisms use habitats and intrinsic resources to survive, reproduce and ultimately affect fitness. For much of the 20th century, research was mainly on studying species during the breeding season; however, by the 1970s, the focus had changed to understanding migratory waterfowl throughout their annual cycle and range in Europe and North America. Autumn and winter are considered the non-breeding seasons, but habitat and resource use through these seasons is crucial for completing spring migration and subsequent breeding. Here we review the literature on autumnal and winter habitat use by Nearctic and Palearctic waterfowl to determine characteristics of important landscapes and habitats for the birds during autumn migration and in winter. Selection of habitats and resources is discussed (when literature permits) in relation to Johnson's (1980) model of hierarchical habitat selection. Habitat use by selected species or groups of waterfowl is also reviewed, and important areas for future research into habitat ecology are identified. We suggest that the greatest lack of understanding of waterfowl habitat selection is an ongoing inability to determine what habitats and intrinsic resources, at multiple scales, are truly available to birds, an essential metric in quantifying "selection" accurately. Other significant challenges that impede gaining knowledge of waterfowl ecology in the northern hemisphere are also described. Nonetheless, continued technological improvements and engagement of diverse interdisciplinary professional expertise will further refine understanding of waterfowl ecology and conservation at continental scales.

**Key words:** autumn, habitat use, migration, selection, waterfowl, winter.

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Understanding how wildlife and especially birds use habitats and resources to survive and reproduce (*i.e.* promote fitness; *sensu* Kaminski & Elmberg 2014) has long been the subject of ecological research (Darwin 1859; Lack 1944; Morrison *et al.* 1992). Studies of waterfowl habitat use and selection are well represented within the substantial avian literature (Block & Brennan 1993; Kaminski & Elmberg 2014). David Lack's (1966) early reference to habitat selection remains valid today, and visionaries such as Lack and also Fretwell (1972) further hypothesised that non-breeding habitats and resources may be important limiting factors for birds of the northern hemisphere, especially migratory species such as waterfowl. Conditions at non-breeding habitats (*e.g.* winter wetlands) correlate with waterfowl recruitment (Heitmeyer & Fredrickson 1981; Nichols *et al.* 1983; Kaminski & Gluesing 1987; Raveling & Heitmeyer 1989; Guillemain *et al.* 2008). However, understanding habitat use and selection by seasonally mobile waterfowl remains challenging, because technology, logistics, economics and other constraints impede monitoring and assessment of resource availability, exploitation and biological outcomes for individuals and populations, from local to flyway scales and cross-seasonally (Elmberg *et al.* 2014; Kaminski & Elmberg 2014; Sedinger & Alisauskas 2014).

The number of waterfowl species and different populations, and their abundance and geographic distribution in the Holarctic, makes waterfowl dominant fauna of aquatic and terrestrial systems in the northern hemisphere (Raveling 2004). Many waterfowl species are largely tied to freshwater systems but several use agricultural, estuarine and marine environments (Bellrose 1980; Baldassarre 2014). Some waterfowl habitats are relatively stable and seasonally predictable relative to hydrology (*e.g.* estuarine and lacustrine wetlands; Cowardin *et al.* 1979), whereas other habitats provide food and other resources temporarily but are characteristically dynamic, such as harvested agricultural lands, riverine and palustrine wetlands (Tourenq *et al.* 2001; Fredrickson 2005; Baldassarre & Bolen 2006; Mitsch & Gosselink 2007; O'Neal *et al.* 2010).

Here, classic and contemporary literature that revealed habitat and associated resource use by Holarctic waterfowl during autumn and winter is reviewed, with emphasis on the latter season of the annual cycle. The review does not provide an exhaustive summary of habitat and resource use by each species or group of waterfowl, but gives an overview focusing on habitat use by non-breeding waterfowl from macro- to finer spatial scales, when available information permitted such coverage (*sensu* Johnson 1980; Kaminski & Elmberg 2014). Space limitations required us to review a selected group of waterfowl species and tribes, but planning is underway to address non-breeding seasonal ecology of lesser known taxa (*e.g. Cairini* sp., *Dendrocygnini* sp. and *Anas fulvigula*) and better known or more widely distributed Nearctic species in a future publication (*e.g. A. americana, crecca, clypeata, strepera, rubripes* and *Branta canadensis*). We begin with a conceptual overview of autumn migration applicable to Nearctic and Palearctic waterfowl, followed by a review of selected eco-regions important to non-breeding waterfowl in the Holarctic and the aforementioned review of selected species or groups of ducks, geese and swans. Finally, currently perceived challenges in studying habitat selection by non-breeding waterfowl are conveyed to stimulate further research and conservation of these birds and their habitats in the northern hemisphere and worldwide.

## Hierarchical habitat use and selection

Kaminski & Elmberg's (2014) conceptual review of hierarchical habitat selection (*sensu* Johnson 1980), indicated that habitat use and selection by migratory birds, such as most waterfowl, can be envisioned as a multi-stage, spatio-temporal process from macro- to micro-scales throughout the birds' annual cycle and range. Migratory waterfowl seemingly make 1st order selection of geographic regions, such as those important to and used by the birds during breeding and non-breeding seasons (Johnson 1980; Baldassarre & Bolen 2006). Within 1st order occupied regions, waterfowl make 2nd order selections of wetland systems (Cowardin *et al.* 1979) and possibly associated landscapes for some species adapted to terrestrial habitats (*e.g.* arable lands). Next, waterfowl make 3rd order selections of local, site-specific wetlands or other locations in their seasonal home range, and finally 4th order selections of microhabitats where individuals may roost, forage or engage in other activities to acquire food or other resources, including mates (Wiens 1973; Johnson 1980; Kaminski & Weller 1992; Baldassarre & Bolen 2006). A reversal of this process from micro- to macro-habitats also can be envisioned, as birds depart micro-habitats to disperse or migrate to different regions.

## Autumn migration

Avian migration involves complex physiological, behavioural, genetic and ecological influences at individual and flock levels, which can influence population dynamics and demography (Dingle & Drake 2007). Numerous publications focus on avian migration (*e.g.* Dingle 1996; Dingle & Drake 2007; Newton 2007; Stafford *et al.* 2014), but a disproportionate number address passerines, while relatively few consider waterbirds. This reality is surprising given the well-known migratory nature of most Holarctic waterfowl (Arzel *et al.* 2006).

Migration involves large-scale movements from breeding to non-breeding grounds and vernal returns to breeding grounds (Salewski & Bruderer 2007; Zink 2011). Autumnal migration may be considered endogenously and exogenously influenced seasonal movements of birds between breeding and non-breeding areas (Alerstam & Lindström 1990; Dingle 1996; Salewski & Bruderer 2007). A perplexing aspect of autumn migration in waterfowl is that timing of departure in birds is especially complicated (O'Neal *et al.* 2010; Krementz *et al.* 2012). Long-migrant passerines typically exhibit a time-minimisation strategy (Dänhardt & Lindström 2001; O'Neal *et al.* 2010), and although geese and swans refuel at staging sites for shorter periods in autumn than in spring (Madsen 1980; Luigujõe *et al.* 1996; Beekman *et al.* 2002), some ducks, such as larger-bodied species like Mallard *Anas platyrhynchos*, may remain at mid-migration stopovers for weeks or longer despite harsh weather conditions that seemingly would stimulate migration (Bellrose & Crompton 1970; O'Neal *et al.* 2010; Schummer *et al.* 2010; Krementz *et al.* 2012; Dalby 2013). Moreover, autumn migration and winter habitat use are further complicated by habitat availability and quality and human-related disturbance (*e.g.* Väänänen 2001; Roshier *et al.* 2006; Legagneux *et al.* 2009; O'Neal *et al.* 2010; St. James *et al.* 2013).

Life histories of waterfowl vary considerably among species and confound simple explanations of migration patterns. For instance, although body size influences migration and habitat use (Raveling 2004), American Black Duck *Anas rubripes* (1,100 g; Zammuto 1986; Baldassarre 2014) overlaps in time and space with American Green-winged Teal *A. crecca carolinensis* (318 g; Zammuto 1986), the smallest dabbling duck species, during migration and winter (Bellrose 1980, Baldassarre & Bolen 2006). Conversely, Blue-winged Teal *A. discors* (363 g; Zammuto 1986), although ~12% heavier than Green-winged Teal, winter at more southerly latitudes (≤ 30°N; Thompson & Baldassarre 1990). Clearly, waterfowl migration patterns do not strictly follow ecological generalisations such as Bergmann's Rule (Bergmann 1847).

Many Palearctic waterfowl converge from Fenno-Scandian and Russian breeding grounds toward the Baltic Sea, where they use various habitats as staging sites before gradually moving south during winter. Some birds such as Eurasian Teal *A. crecca crecca* move by successive small flights in early autumn, whilst Mallard lag behind and move later in less numerous but longer flights (Dalby 2013). Others, such as Northern Pintail *A. acuta*, may be nomadic and seek newly flooded but ephemeral habitats in autumn (Bellrose 1980), whereas Mallard may have protracted migrations (Bellrose 1980; Krementz *et al.* 2012).

Movements, site fidelity and turnover rates of waterfowl during autumn-winter are likely to reveal patterns of habitat suitability and trade-offs made by waterfowl during these periods of the annual cycle (Rodway 2007). Winter site fidelity is known to be strong in geese and swans (Owen 1980) but of lesser importance in ducks, which exhibit greater spatio-temporal plasticity in habitat use (Mulhern *et al.* 1985; Robertson & Cooke 1999). Moreover, interspecific comparisons of winter philopatry are confounded by vast differences in the size of regions investigated (Robertson & Cooke 1999). In Europe, studies of individually-marked Eurasian Teal highlighted significant wintering site fidelity among and within winters (Guillemain *et al.* 2009; Guillemain *et al.* 2010a), suggesting that birds were able to evaluate site quality and adapt their use of traditional wintering areas, perhaps resulting in increased individual fitness. Of course, such traditions may be jeopardised if abrupt habitat changes occur. Indeed, the ecology of waterfowl migration in the northern hemisphere remains a frontier for future scientific investigation (Arzel *et al.* 2006).

## Selected important Holarctic regions for non-breeding waterfowl

### Eastern United States

The eastern U.S. historically has been an important region for migrating and wintering waterfowl, particularly lacustrine and estuarine coastal wetlands and deepwater habitats (Cowardin *et al.* 1979; Bellrose 1980). The region of the Atlantic Coast Joint Venture (ACJV) encompasses 17 states in the Atlantic Flyway and is the most densely human-populated area in the conterminous U.S., wherein about 35% of the population resides (ACJV 2009).

Landscape diversity in this region includes ~22% agricultural land and 25% wetlands, which together support ~37 native species of waterfowl (ACJV 2009). Considering 2nd order habitat selection within this region, estuarine systems of coastal Maine are important to wintering American Black Duck, Common Eider *Somateria mollissima* and scoters *Melanitta* sp. that use sheltered ice-free areas for foraging and loafing (ACJV 2005), while fringes of saltmarshes and mudflats are important to Mallard and other dabbling ducks (Jorde *et al.* 1984). Barrier beaches, back-barrier coastal lagoons and salt marshes of Long Island and New Jersey provide additional important winter habitats for American Black Duck and Brent Geese *Branta bernicla* (ACJV 2005; Plattner *et al.* 2010). Farther south exists the Chesapeake Bay, the largest estuary in the conterminous U.S. with a watershed that drains 165,760 km$^2$, along with North Carolina Sounds, natural and artificial lakes and reservoirs, flooded bottomland hardwoods, Carolina bays and estuarine and salt marshes that provide habitat for a diversity of ducks, geese and swans (Hindman & Stotts 1989).

Additionally, South Carolina and Georgia provide habitat for wintering dabbling, diving and sea ducks (Gordon *et al.* 1989; ACJV 2005). South Carolina alone winters ~30% of all dabbling ducks in the Atlantic Flyway including Green-winged Teal, Northern Shoveler *Anas clypeata*, Mallard, American Wigeon *A. americana* and Northern Pintail (Gordon *et al.* 1989). In Florida, the St. John's and Indian Rivers basins provide important waterfowl habitat, supporting nearly 400,000 ducks during winter (ACJV 2005). Freshwater lakes, such as Lake Okeechobee, also provide important wintering habitats for many waterfowl, including Lesser Scaup *Aythta affinis*, Ring-necked Duck *A. collaris*, American Wigeon, and Blue-winged Teal (Johnson & Montalbano 1989).

## Mississippi Alluvial Valley

Largely forested prior to settlement by Europeans in the 19th century, flood control for agriculture and human inhabitation influenced a nearly 80% loss of lowland forests in the Mississippi Alluvial Valley (MAV) by the late 20th century, with only highly fragmented tracts remaining today (MacDonald *et al.* 1979; Klimas *et al.* 2009). The MAV contains flooded croplands, wetlands, deep water habitats and aquaculture ponds that are important to migrating and wintering ducks and geese (Cowardin *et al.* 1979; Christopher *et al.* 1988; Reinecke *et al.* 1989; Stafford *et al.* 2006; Kross *et al.* 2008; Feaga 2013). Swans (*e.g.* Trumpeter Swans *Cygnus buccinator*) are rarely sighted in winter in the MAV (R.M. Kaminski, pers. obs.; MAV Christmas Bird Counts unpubl. data).

Within the flooded agricultural landscape (including the aquaculture ponds), migrating and wintering waterfowl use 2nd order lacustrine (*e.g.* oxbow and watershed lakes, reservoirs), palustrine (*e.g.* forested and moist-soil wetlands) and riverine systems in the MAV (*e.g.* Mississippi River and tributaries; Cowardin *et al.* 1979; Mitsch & Gosselink 2007). Considering 3rd order habitat use of agricultural lands and wetlands within 2nd order systems, Reinecke *et al.* (1992) reported that over half of the Mallard observed during aerial surveys across most of the MAV used flooded rice and soybean fields during winters 1987–1990. Subsequently, during the early 2000s, Pearse *et al.* (2012) reported that greatest densities of Mallard in the Mississippi portion of the MAV during winter were observed in habitat complexes composed of 50% flooded cropland, 20% hardwood or scrub-shrub wetlands, 20% moist-soil and other emergent wetlands and 10% permanent water bodies (*e.g.* rivers, lakes, ponds). Greatest densities of other dabbling duck species were also associated with a similar habitat composition (Pearse *et al.* 2012).

Waterfowl associations with flooded cropland might be expected given that the MAV is now largely an agricultural landscape. Despite losses of natural wetlands in the MAV and continentally (Mitsch & Gosselink 2007), migrating and wintering waterfowl have adapted to flooded agricultural lands and make significant use of them in the MAV to meet nutritional and other physiological needs (Delnicki & Reinecke 1986; Reinecke *et al.* 1989; O'Neal *et al.* 2010). Indeed, ricelands in the MAV are critical for meeting seasonal requirements of waterfowl using this region (Stafford *et al.* 2006). In the late 1970s and early 1980s, Delnicki & Reinecke (1986), studying food use and body weight, estimated that rice represented > 41% of total food intake by Mallard. However, because rice, soybean, and other seed crops are planted and harvested earlier nowadays in the MAV than during the 20th century, deterioration of waste seed occurs because of germination, decomposition and consumption by non-waterfowl species after harvest but before major wintering flocks arrive in the MAV (Stafford *et al.* 2006; Foster *et al.* 2010; Petrie *et al.* 2014). Reduction in waste rice from harvest through late autumn–early winter in the MAV is estimated at 71–99% (Manley *et al.*; Stafford *et al.* 2006). Despite reduced availability of waste rice in harvested fields in the region, flooded rice fields however have structural characteristics similar to natural wetlands (Elphick 2000; Huner *et al.* 2002; Marty 2013). The mid-winter population goal for the Lower Mississippi Valley Joint Venture of the North American Waterfowl Management Plant (LMVJV) is > 7.8 million dabbling ducks, and winter-flooded rice fields provide ~11% of all food energy available to dabbling ducks in flooded habitats in the LMVJV (Petrie *et al.* 2014). Approximately 20% of the 748,668 ha of ricelands is winter-flooded in the LMVJV (Petrie *et al.* 2014). If the LMVJV rice fields were able to produce a second harvested crop intra-seasonally as in Louisiana and Texas (*i.e.* ratoon crop, Marty 2013), the amount of food available to dabbling ducks from the flooded fields in the LMVJV would increase 12-fold (Petrie *et al.* 2014). Development of rice varieties and other crops with ability to ratoon at latitudes within the MAV would increase substantially the abundance of waste grain following harvest and benefit migrating and wintering waterfowl (Wiseman *et al.* 2010; Petrie *et al.* 2014; Marty 2013).

Despite dominant coverage of agricultural land in the MAV, Mallard and other waterfowl use 3rd and 4th order wetland sites in the MAV (Reinecke *et al.* 1989). Reinecke *et al.* (1992) reported that Mallard used forested wetlands (3–11%) and moist-soil wetlands (3–29%) within and among winters. Additionally, Davis & Afton (2010), working in the Louisiana portion of the MAV, reported that radio-marked female Mallard selected forested wetlands and suggested that continued restoration and establishment of these habitats should benefit females. However, they did not report any relationships between Mallard winter survival or other correlates of fitness that might implicate benefits resulting from female use of forested wetlands. Subsequently, Lancaster (2013), working in the Mississippi portion of the MAV, investigated habitat-related survival of radio-marked female Mallard. Greatest rates of winter survival (≥ 75%) were exhibited by females that used habitat complexes composed mostly of forested and emergent wetlands (86% combined) and 12% cropland, which was notable considering that most of the MAV landscape now is cropland (Lancaster 2013; Kaminski & Davis 2014). Thus, although Mallard may be considered habitat generalists, they also use certain habitats disproportionately, affording increased fitness prospects consistent with the concept of habitat suitability (*sensu* Fretwell 1972; Kaminski & Elmberg 2014).

Considering 4th order microhabitats, Mallard and Wood Duck *Aix sponsa* differentially used flooded hardwood bottomlands in the Interior Flatwoods and MAV in Mississippi during winter. Mallard used microhabitats that contained less woody understory cover, whereas Wood Duck were associated with microhabitats of increased understory vegetation (Kaminski *et al.* 1993). Within moist-soil wetlands in the MAV, dabbling ducks of several species foraged in experimental plots with water depths ranging from 3–16 cm (Hagy & Kaminski 2012). Such a range of depths may facilitate forage acquisition by a diversity of species using a common habitat, at least until food depletion occurs (Greer *et al.* 2009; Hagy *et al.* 2014).

In addition to flooded croplands and natural wetlands in the MAV, aquaculture ponds for production of Channel Catfish *Ictalurus punctatus* and bait fish have become important staging and wintering habitats used by dabbling and diving ducks since their construction in the 1970s (Christopher *et al.* 1988; Reinecke *et al.* 1989; Wooten & Werner 2004). Species of waterfowl commonly using catfish ponds include Lesser Scaup *Aythya affinis*, Ruddy Duck *Oxyura jamaicensis* and Northern Shoveler, along with lesser abundances of Mallard, Gadwall *A. strepera*, and introduced resident Giant Canada Geese *Branta canadensis maxima* (Christopher *et al.* 1988; Dubovsky & Kaminski 1992; Vest *et al.* 2006, Feaga 2013). Dubovsky & Kaminski (1992) estimated that 150,000 ducks used catfish ponds in Mississippi, with an average of 100,000 individuals using ponds weekly in the mid-1980s. Wooten & Werner (2004) collected Lesser Scaup from Arkansas baitfish ponds and reported scaup primarily ingested *Chironomidae* larvae, but ~25% of collected birds contained fish biomass or bones.

Because of competition from foreign markets, infrastructural and other costs, catfish aquaculture has declined in the MAV (U.S. Department Agriculture 2010). There were 64,000 ha of ponds in Mississippi, Louisiana and Arkansas in 2001, but only 25,000 ha remained in operation in those states by 2012 (Lehnen & Krementz 2013). Feaga (2013) reported that migrating and wintering waterfowl and other waterbirds occurred in densities on catfish production impoundments (~130 birds/ha) similar to idled impoundments (~120 birds/ha). However, different bird communities existed in production *versus* idled production ponds, the latter now managed to provide emergent vegetation, mudflats and shallow wetland areas < 30 cm during summer–winter wetland birds (Feaga 2013; Kaminski & Davis 2014). Diving and dabbling ducks and American Coot *Fulica americana* were primary users of production aquaculture impoundments (Dubovsky & Kaminski 1992; Feaga 2013), whereas idled impoundments were used by over 40 species of ducks, shorebirds, waders and other waterbirds (Feaga 2013; Kaminski & Davis 2014).

## Louisiana-Texas Gulf Coast

The coastal tallgrass prairies of Louisiana and Texas once covered over 1 million ha (Chabreck *et al.* 1989; Hobaugh *et al.* 1989). They have slight topography, relatively impervious soils and thus seasonal wetlands (Smeins *et al.* 1991; Petrie *et al.* 2014). Winter rains and tropical storms in summer–autumn periodically inundate basins and provide habitat for numerous migrating and wintering waterfowl (Petrie *et al.* 2014).

Fresh and intermediate brackish marshes have been among the greatest wetland losses in the coastal prairies; ~100,000 ha of non-farmed freshwater wetlands have been lost in the coastal plains of Texas since the mid-1940s (Moulton *et al.* 1997). Conversion of rice agriculture to cotton and soybean production has further reduced important habitats for waterfowl (Anderson & Ballard 2006). Gulf coastal wetlands are critical to several guilds of wintering waterfowl (Weller 1964; Chabreck *et al.* 1989; Hobaugh *et al.* 1989; Marty 2013), and an estimated 19% of all waterfowl wintering in the U.S. use marshes in the Louisiana Gulf Coast (Michot 1996; Bolduc & Afton 2004). The Texas Mid-Coast once wintered 78% of the Northern Pintail in the Central Flyway (Ballard *et al.* 2004). Contemporary estimates of midwinter population goals for the Gulf Coast JV region include > 5.6 million dabbling ducks (Petrie *et al.* 2014).

Considering 2nd and 3rd order habitat selection, freshwater and intermediate marshes along the Gulf of Mexico are perhaps the most important wetland habitats for waterfowl in the region (Chabreck *et al.* 1989; Batzer & Baldwin 2012). Brackish marshes are the most extensive habitat and considered historical habitats for wintering Snow Geese *Anser caerulescens* (Chabreck *et al.* 1989; Batzer & Baldwin 2012), but salt marsh habitats are generally regarded as less favourable to waterfowl in Gulf coastal systems (Williams III & Chabreck 1986; Batzer & Baldwin 2012). In addition to these, lakes (*e.g.* Grand, White), bays (*e.g.* Atchafalaya, Terrebonne) and off-shore habitats have been important historically for scaup and other diving and sea ducks in the Gulf region (Harmon 1962; Afton & Anderson 2001).

Scaup wintering off-shore in Louisiana have comprised 50–86% of the total wintering population and were much more abundant off-shore than in in-shore habitats in January (Kinney 2004). Kinney (2004) flew transect surveys and determined that only about 15% of scaup were detected in some years by traditional Midwinter Waterfowl Surveys. One hypothesis for scaup wintering farther off-shore is that Surf Clams *Mulinia lateralis* were historically a preferred food for the species (Harmon 1962; Kinney 2004) and recent increases in hypoxic areas in the near-shore waters of the Gulf may be causing scaup to venture farther off-shore for food.

Along the Texas Gulf Coast, the Laguna Madre is a large shallow lagoon that contains ~80% of the seagrass communities along the Texas coast (Ballard *et al.* 2010). The dominant species is Shoal Grass *Halodule wrightii* and ~80% of the continental Redhead *Aythya americana* population winters in the region, primarily because of seagrasses (Division: Angiospermae) and associated habitats (Weller 1964; Mitchell *et al.* 1994; Michot *et al.* 2006; Ballard *et al.* 2010). Several studies have documented the importance of proximate inland freshwater ponds to Redhead and other ducks including Lesser Scaup (Adair *et al.* 1996; Michot *et al.* 2006; Ballard *et al.* 2010). The proximity of coastal ponds to seagrass foraging areas on the Gulf Coast is important, as Redhead were never observed using ponds > 5.7 km from the shoreline or > 8.1 km from the nearest foraging area (Ballard *et al.* 2010). Thus, proximity of freshwater ponds to seagrass beds in the Laguna Madre is an example of a critical synergistic habitat association, particularly in drier winters (Ballard *et al.* 2010).

## United States Great Plains

The Playa Lakes Region (PLR) contains 60,000–100,000 playa lakes or shallow wetlands that generally occur at the bottom of large watersheds and are formed by wind and water dissolution processes (Smith 2003; Venne *et al.* 2008). Playa wetlands range in size from < 1 ha to > 300 ha, extend from Wyoming and Nebraska to Texas and New Mexico, and are habitat to a wide diversity of life forms including waterfowl (Playa Lakes Joint Venture 2014). Historic native grassland has largely been replaced with arable crops, and subsequent erosion of topsoil has contributed to sedimentation of ~90% of all playas in the Southern High Plains (SHP; Venne *et al.* 2008). Moreover, ~80,000 playas throughout the Great Plains states are currently incapable of recharging the Ogallala aquifer (Playa Lakes Joint Venture 2014). Historically, one-third of the Central Flyway Northern Pintail population (~300,000 birds) used playa lakes in the SHP, but this population has declined 47% since 1977 (Bellrose 1980; Luo *et al.* 1997; Haukos 2004; Moon *et al.* 2007). Concomitantly, body condition of pintail in the PLR has declined considerably since the mid-1980s (Moon *et al.* 2007).

The SHP is a southern extension of the PLR and is a critical region to waterfowl, once containing 25,000–30,000 wetlands (Smith 2003; Baldassarre & Bolen 2006; Venne *et al.* 2008). Obenberger (1982) studied several species of dabbling ducks from autumn–late winter 1980–1982 and reported that ducks generally had a bimodal migration. Migration phenology of Northern Pintail and Green-winged Teal peaked in November, and autumn abundances were at least double their greatest numbers during vernal peaks. Nearly 30 years later, Baar *et al.* (2008) conducted similar research in the SHP and observed that duck use of playas was much more intermittent, protracted or less intensive compared to previous decades. Baar *et al.* (2008) offered two possible explanations for these patterns. First, abundance of playa wetlands, irrigation ponds and tailwater reservoirs were greatly reduced, and playas have become more rainfall dependent (Smith 2003; Baar *et al.* 2008). Second, playas have been subjected to significant sedimentation, with negative impacts to hydrologic patterns and function (Smith 2003). Moon & Haukos (2006) attributed declining body condition of Northern Pintail to harassment and stress, resulting from increased movements by hunters pursuing waterfowl and Ring-necked Pheasant *Phasianus colchicus* (Baar *et al.* 2008).

Generally, evidence suggests that important waterfowl foods, such as waste agricultural or natural seeds, are becoming depleted in early winter in the SHP (Baldassarre & Bolen 1984; Bolen *et al.* 1989; Smith & Sheeley 1993; Moon & Haukos 2006). As a consequence, exploitation of these environments by dabbling and other ducks may be more limited during late winter and spring (Baar *et al.* 2008) compared with prior decades (Obenberger 1982). Dedicated conservation programmes have been championed and are needed in the SHP (Haukos & Smith 2003; Smith 2003).

## Central Valley of California

California always has been one of the most important regions for wintering waterfowl in North America (Gilmer *et al.* 1982; Miller 1986; Heitmeyer *et al.* 1989; Fleskes *et al.* 2005; Miller *et al.* 2010). The state has lost ~95% of its historic wetlands (Central Valley Joint Venture 2006) but continues to support millions of non-breeding waterfowl. Within California, the Central Valley provides critical wetland and agricultural habitat for migrating and wintering waterfowl and was the focus of one of the original Joint Ventures of the North American Waterfowl Management Plan (NAWMP 1986). The Central Valley encompasses ~4.1 million ha, stretching 724 km north to south and 64 km east to west. The valley is dominated by two riverine systems – the Sacramento River and the San Joaquin River, which meet at the Delta then flow into the Pacific Ocean past the Suisun Marsh, one of the largest contiguous brackish marshes in the western United States.

The hydrology of the valley determines the main habitat types and influences seasonal and inter-annual patterns of waterfowl use (Fleskes 2012). However, hydrology has been altered drastically from agriculture and urban growth and caused considerable changes in distribution of waterfowl habitats. Before the 1849 Gold Rush, the valley contained > 1.6 million ha of wetland habitat (Central Valley Joint Venture 2006). Most of these wetlands were seasonal, inundated by riverine flooding in the valley, bordered by expansive riparian and grassland habitats, which may have supported 20–40 million waterfowl during migrations and winter.

Seasonal and permanent wetlands in the Central Valley are distributed in four sub-regions: the southern San Joaquin Valley (including Tulare Basin, which held the now dry Tulare Lake, once the largest freshwater lake west of Mississippi; Fleskes 2012), the northern Sacramento Valley, the Delta and the Suisun Marsh. Historically, many waterfowl wintering in California would migrate first to Tulare Lake, a vast shallow complex of seasonal and permanent marshes. As winter progressed birds moved north, through the San Joaquin Valley, Delta and Suisun Marsh into the Sacramento Valley. Prior to land conversion, ~40% of waterfowl habitat occurred in the San Joaquin Valley (including Tulare Basin), while the remaining 60% occurred in the Sacramento Valley, Delta and Suisun Marsh (Fleskes *et al.* 2005). By approximately 1900, the Tulare lakebeds were effectively drained by diversion of water for agriculture, and the lakebeds now remain dry in all but extremely wet years. Wetlands in the San Joaquin and Sacramento Valleys were also converted to agricultural land, leading to cotton, orchard, vegetable and rice production in the Sacramento Valley. In the Delta, islands were leveed to grow corn, barley and other grain crops, some of which have value to ducks and geese.

Brackish marsh wetlands in the Suisun Marsh historically were significant to wintering waterfowl, but populations of dabbling ducks and geese there have declined. The Suisun Marsh currently provides wintering habitat for > 60,000 waterfowl, of which dabbling ducks are the most numerous (55,000), followed by diving ducks, geese, sea ducks, and swans (Ackerman *et al.* 2014). Following decades of considerable landscape changes, the Central Valley is left with merely 162,000 ha of wetlands nested within a largely agricultural matrix.

Most existing wetland habitat in the valley is managed and comprises seasonal, semi-permanent and permanent wetlands. Seasonal wetlands are flooded in autumn for waterfowl and other waterbirds and drawn down in late winter. Many wetlands are managed as waterfowl hunting clubs or state and federal wildlife areas or refuges. Seasonal wetlands provide critical foraging habitat for non-breeding waterfowl. These wetlands are managed annually using several methods (*e.g.* disking, irrigation and water management) to promote moist-soil plants such as Watergrass *Echinochloa crusgalli*, smartweed *Polygonum* sp. and Swamp Timothy *Crypsis schoenoides* (Heitmeyer *et al.* 1989). Semi-permanent wetlands are flooded from autumn to early July, while permanent wetlands are flooded throughout the year (Central Valley Joint Venture 2006). Semi-permanent and permanent wetlands produce less food, but provide important roosting and brood habitat for locally breeding ducks, mostly Mallard and Gadwall.

The most significant change to waterfowl habitats in the Central Valley over recent decades has been the development of rice agriculture, particularly in the Sacramento Valley. Planted rice acreage has increased from nearly 41,000 ha (1930s) to almost 243,000 ha, and now averages > 202,000 ha (Petrie *et al.* 2014). Waste grain remaining in fields after harvest provides a valuable food source for wintering waterfowl (Eadie *et al.* 2008). Along with the increase of planted rice, there has been a significant change in management of residual rice straw after harvest. Before the 1990s, fire was the primary method for rice straw disposal.

However, with air quality concerns, the Rice Straw Burning Reduction Act of 1991 mandated that burning of straw be reduced and currently less than 10% of all harvested rice fields are currently burned. As an alternative, rice growers turned to post-harvest flooding, accompanied by disking, rolling or chopping of straw. The result was that flooded rice fields provided valuable foraging habitat to a diversity of dabbling ducks and geese. At the peak, > 141,000 ha of harvested rice fields were flooded in autumn, nearly 70% of the planted rice acreage (Central Valley Joint Venture 2006; Petrie *et al.* 2014).

Waterfowl wintering in the Central Valley have responded strongly to these changes at both 2nd and 3rd orders of habitat selection. Timing and distribution of 2nd order selection by waterfowl have been altered considerably with the draining of Tulare Lake and increase of rice agriculture in the northern reaches of the valley. Fleskes *et al.* (2005) reported that the total area of croplands intentionally flooded in winter increased by 157% in the Sacramento Valley and 58% in the Delta, but declined by 23% in the San Joaquin Valley between 1973 and 2000, leaving only 3% of the total winter-flooded agricultural land in the latter region. In response, birds have shifted winter distributions northward. Fleskes *et al.* (2005) conducted extensive surveys and radio-telemetry in 1998–2000 and compared results to data from 1973–1982 (Heitmeyer *et al.* 1989; Miller *et al.* 1993; Miller *et al.* 1995). The recent research indicated that the percentage of dabbling ducks using the Tulare basin and the San Joaquin Valley declined, especially in late winter, while use increased in the Sacramento Valley. Cinnamon Teal *Anas cyanoptera* were an exception and did not shift northward. In contrast to dabbling ducks, the percentage of diving ducks using the San Joaquin and Tulare Basins increased concurrently with a decrease in diving ducks using the Suisun Marsh and Delta. Use of the Suisun Delta and San Joaquin Valley declined for geese, with concomitantly large increases in the Sacramento Valley. Thus, the Central Valley has experienced substantial shifts in the distributions of all waterfowl, reflecting significant changes at the 2nd order level of habitat selection.

Most of these distributional shifts of waterfowl in the Central Valley have been driven by the large-scale changes in habitat availability and 3rd (and possibly 4th) order levels of habitat selection. Currently, dabbling ducks in the Central Valley rely on three major habitat types: 1) flooded harvested rice fields, 2) managed seasonal wetlands, and 3) flooded and unflooded harvested corn fields (Central Valley Joint Venture 2006). Geese in the valley also use unflooded rice fields and uplands. Petrie *et al.* (2014) estimated that winter-flooded rice fields provided 44% of all food energy available to dabbling ducks in flooded habitats in the Central Valley, while flooded and unflooded rice fields provided 49% of all food energy available to dark geese but 73% of all food energy for white geese. These results were corroborated by Fleskes *et al.* (2005); they reported the importance of agricultural habitat (relative to managed wetlands) for Northern Pintail, Mallard and Greater White-fronted Geese *Anser albifrons* was greater than 20–30 years ago, presumably as birds increased their use of flooded rice fields.

In addition to the above patterns, the importance of managed wetlands has increased in the Suisun Marsh. Most waterfowl that winter in Suisun Marsh are dabbling ducks, which primarily use managed wetland habitats provided by duck hunting clubs and state wildlife areas (Ackerman *et al.* 2014). Coates *et al.* (2012) radio-marked and relocated 330 female Northern Pintail in the Suisun Marsh to estimate resource selection during non-breeding months and found strong evidence for selection of managed wetlands. Ackerman *et al.* (2014) reanalysed Northern Pintail telemetry data to examine habitat selection. They compared spatial patterns of habitat use by ducks to availability of habitats at two spatial scales and found that Northern Pintail strongly selected managed wetland habitats at both small and large scales. Further, Northern Pintail avoided tidal marshes, bays, sloughs and some other habitats (Ackerman *et al.* 2014). These results have important implications for Northern Pintail given current efforts to restore large portions of the Suisun Marsh to tidal wetlands. The consequences for dabbling ducks using the marsh have not yet been thoroughly assessed, and loss of managed wetlands in the Suisun Marsh remain a concern for waterfowl managers (Ackerman *et al.* 2014).

Patterns of habitat selection by waterfowl in the Central Valley represent large-scale shifts in the area and type of habitats available; as a consequence, significant changes in 2nd and 3rd order habitat selection have occurred by many species of ducks and geese. Most remaining wetlands are intensively managed to produce seed-producing moist-soil plants. The decline of Northern Pintail has resulted in management of seasonal wetlands toward more densely vegetated marshes favoured by Mallard. This technique has reduced amount of sparse and short vegetation which is likely more representative of seasonal flooded wetlands sought historically by Northern Pintail. The greatest recent change in the Central Valley has been the considerable increase in rice acreage, especially in the Sacramento Valley. This change has led to a northern shift from the San Joaquin Valley by most species (2nd order habitat selection) and a substantial increase in use of flooded and unflooded rice fields as foraging habitat (3rd order). Indeed, rice landscapes have become so important to wintering waterfowl that decline or loss of this agriculture would seem catastrophic to Northern Pintail and likely other wetland-dependent birds (Petrie *et al.* 2014). Nearly half of all duck-use-days in the U.S. portion of the Pacific Flyway occur in the Central Valley, and loss of rice would have continental impacts on Northern Pintail and other waterfowl using ricelands (Petrie *et al.* 2014). However, the future of flooded rice as winter habitat for waterfowl is in question with recent record droughts, water requirements for in-stream flows to meet needs of several species of federally endangered fish, and ever-growing urban demands. Petrie *et al.* (2014) estimated that > 75,000 ha of additional managed moist-soil wetlands would be required to replace the waterfowl food value provided by existing ricelands in the Central Valley. While rice agriculture is unlikely to disappear from the valley, the total acreage and the way it is managed post-harvest are uncertain.

Understanding the shifting mosaic of available winter habitats and bird responses will be an ongoing research need to guide conservation initiatives.

## Pacific Coast

San Francisco Bay is the largest estuary along the west coast of the continental U.S. and historically important migration and wintering grounds for sea and other diving ducks (Conomos *et al.* 1985; Hothem *et al.* 1998). More than 85% of the tidal wetlands of the Bay have been lost to agriculture and development in the 20th Century (Nichols *et al.* 1986; Hothem *et al.* 1998). Anthropogenic changes and impacts have affected numerous waterfowl and other birds, including Canvasback *Aythya valisineria* whose overwintering numbers dropped by 50% during the 1970s–1990s (Hothem *et al.* 1998). Despite habitat modifications, San Francisco Bay may harbour nearly 50% of the total population of several diving duck species during winter (Accurso 1992; Brand *et al.* 2014). Given the history of mining in California, the position of the San Francisco Bay makes it susceptible to accumulating contaminants such as mercury, cadmium and selenium (Heinz *et al.* 1989; Hothem *et al.* 1998).

Farther up the northern California coast, the coastal lowlands are important migration and wintering areas for > 20 species of waterfowl, with populations ranging from 25,000–100,000 birds per day from autumn through spring (Pacific Coast Joint Venture 2004). Humboldt Bay is particularly important for brant because of its extensive Common Eelgrass *Zostera marina* beds. An estimated > 40% of the Pacific Flyway population of brant use Humboldt Bay as a migratory stopover from late February through to mid-April.

## Inter-mountain West and Great Salt Lake

The Inter-mountain West region comprises two regions of special importance to non-breeding waterfowl: Southern Oregon Northeastern California (SONEC), including the Klamath Basin, and the Great Salt Lake. The SONEC region covers approximately 10% of the Great Basin, although waterfowl habitat comprises a much lower percentage (Petrie *et al.* 2013). Historically, peak waterfowl abundance occurred during autumn and spring migration. Migrating waterfowl in autumn likely would have experienced dry conditions and were probably restricted to a few large complexes of permanent or semi-permanent wetlands (Petrie *et al.* 2013). Few birds remained over winter because of the below-freezing winter temperatures. Today, nearly all autumn and winter waterfowl habitat in SONEC occurs on public land. Two refuges are of particular significance: Lower Klamath National Wildlife Refuge (Lower Klamath) and the Tule Lake National Wildlife Refuge (Tule Lake). Although these refuges account for only a fraction of the region, they support a significant portion of the waterfowl that use SONEC in autumn and winter (Kadlec & Smith 1989; Fleskes & Yee 2007). In fact, the Klamath Basin is recognised as a region of continental significance to North American waterfowl populations (NAWMP Plan Committee 2004).

Management of waterfowl habitats on Lower Klamath and Tule Lake refuges depends on water supplies. Increasing demands for water within the Klamath Basin by farmers, native communities and endangered fish have hindered refuges from obtaining sufficient water for waterfowl. A recent analysis using bioenergetics models (TRUEMET) indicated that food resources at Tule Lake were adequate to meet energy needs of diving ducks and swans, but were insufficient for dabbling ducks and geese. Food for dabblers was exhausted in early autumn, well before traditional peak migration in November (Petrie *et al.* 2013). Thus, dabbling duck numbers at Tule Lake have declined significantly since the 1970s. The SONEC region is also critical during spring migration, especially for Northern Pintail. Over 70% of habitat use by radio-marked Northern Pintail in SONEC (outside of the Lower Klamath) occurred on privately-owned habitats, primarily flood-irrigated agriculture (Fleskes *et al.* 2013).

The Great Salt Lake (GSL) is one of the largest wetland complexes in western U.S. and is recognised internationally for its importance to migratory waterfowl (NAWMP Plan Committee 2004). As many as 3–5 million waterfowl migrate through the GSL annually (Petrie *et al.* 2013). The GSL is surrounded by >190,000 ha of wetlands maintained by fresh water from rivers that flow into the basin. The surrounding marshes are extensive and provide rich diversity of invertebrate and plant food resources (Petrie *et al.* 2013). Waterfowl use of the GSL is greatest during late summer – early autumn and also in spring. Peaks occur in September, with birds arriving from northwestern and mid-continent Canada and Alaska, and some from the Prairie Pothole Region. Banding data indicate that many ducks that migrate through the GSL spend the winter in the Central Valley of California and west coast of Mexico (Petrie *et al.* 2013). Use of GSL by waterfowl is lowest in mid-winter but increases during spring. Dynamic ebbs and flows of water and fluctuating lake salinities are significant in maintaining this productive wetland system (Petrie *et al.* 2013).

The Inter-mountain West Joint Venture estimated 17.4 million waterfowl-use-days of the GSL during winter of which dabbling ducks accounted for 74% (Northern Pintail = 39% of dabbling duck use-days; Green-winged Teal = 23%; Mallard = 21% and Northern Shoveler = 11%), while diving ducks comprised 19% of total waterfowl-use-days during winter, with Common Goldeneye *Bucephala clangula* representing 91% of all diving duck use (Petrie *et al.* 2013). Bioenergetics analyses of food supplies in the GSL needed to support migratory waterfowl suggested that seed resources required by dabbling ducks were depleted during autumn migration by late October (Petrie *et al.* 2013). Yet, there may have been > 1 million dabbling ducks alone in the GSL in October and November. These results suggest that dabbling ducks are obtaining unknown but critical energy supplies from perhaps aquatic invertebrates, submerged aquatic vegetation, tubers, or a combination of these (Petrie *et al.* 2013). Petrie *et al.* (2013) concluded that improved understanding and estimation of the spatiotemporal variability of wetland resources and waterfowl resource selection in the GSL system were needed to refine assumptions about the foraging guilds.

## Europe

As in North America, substantial changes in land use and management have occurred in Europe since the early 20th century, where landscapes at staging and wintering areas for waterfowl are now a matrix of agricultural land and other habitats greatly transformed by humans (*e.g.* industrial and residential zones) which envelop small protected areas of remaining wetlands (Thomas 1976; Owen *et al.* 1986; Tamisier & Grillas 1994; Guglielmo *et al.* 2002). Autumn-migrating Western Palearctic waterfowl largely concentrate in a flyway corridor along the Baltic and North Sea coasts (*e.g.* Scott & Rose 1996; Söderquist *et al.* 2013; Calenge *et al.* 2010). Here, the global concerns of sea level rise and other loss of habitat associated with climate change are serious concerns for waterbirds in coastal wetland habitats (*e.g.* Clausen & Clausen 2014), which are further threatened by eutrophication (*e.g.* declines in seagrass beds, Clausen *et al.* 2012) and the encroachment of vegetation that is less nutritious for waterfowl (*e.g.* Common Cord-grass *Spartina anglica*; Percival *et al.* 1998). In contrast, climate warming and increased fertilisation of grasslands in northwest Europe may have enhanced terrestrial habitats for geese, where several populations are flourishing, and some are short-stopping or becoming partly non-migratory (*e.g.* Greylag Geese *Anser anser*, Voslamber *et al.* 2010; Barnacle Goose *Branta leucopsis*, Ganter *et al.* 1999). Hunting restrictions also have likely enhanced the abundance and influenced the distribution and timing of migration of swans and some goose populations. Further south along the flyway, wintering waterfowl, especially ducks (*e.g.* Eurasian Wigeon *Anas penelope*), have largely switched from using marine habitats to freshwater wetlands during daylight hours as the latter have increasingly been managed as nature reserves since the 1950s (*e.g.* Owen & Williams 1976; Guillemain *et al.* 2002). Reserves nowadays not only provide safety from hunting and other human disturbance, but habitats are managed specifically for waterfowl. Yet despite active habitat management, there is an increasing awareness that alien species (*e.g.* Red Swamp Crayfish, *Procambarus clarkia* and Water Primrose *Ludwigia* sp. and Swamp Stonecrop *Crassula helmsii*) are a threat to protected U.S. habitats and European wetlands (*e.g.* Dandelot *et al.* 2005; Meineri *et al.* 2014).

Along the Mediterranean coasts, primary wintering habitats of waterfowl are brackish lakes, lagoons and temporary wetlands. Wetlands of the Mediterranean region have been reduced by 80–90% by urban population growth and conversion to agriculture (Toral & Figuerola 2010). Fortunately, some of these are now rice fields which, as in North America, provide valuable resources to wintering waterfowl (*e.g.* Tamisier & Grillas 1994) and help compensate lost wetland habitats (*e.g.* Tourenq *et al.* 2001; Rendón *et al.* 2008). In the Camargue, southern France, portions of remaining natural wetlands are protected and most are on private estates, wherein temporary and seasonal wetlands are flooded beyond natural hydroperiods to attract waterfowl for hunting and observing.

This practice is detrimental to wetland biodiversity in general, but it has greatly promoted hydrophyte beds on which waterfowl forage (Tamisier & Grillas 1994). Such management is mostly beneficial to herbivorous species (*e.g.* Gadwall) but the other dabblers also benefit from seeds spread as bait in these properties (Brochet *et al.* 2012). Hunting management practices could likely be responsible for considerable improvement of wintering body condition of Common Teal (up to 12%) and other dabbling ducks in past decades (Guillemain *et al.* 2010b).

## Habitat resources of selected northern hemispheric waterfowl

### Dabbling ducks

*Mallard*

Mallard challenge clear distinctions of autumn migration and subsequent winter habitat distributions because of great seasonal and annual variation in settling by individuals or sub-populations within flyways. The breadth of habitats occupied by Mallard in North America is particularly fascinating. In the Sacramento Valley of California, Mallard use agriculturally dominated and largely treeless environments, where patches of seasonally flooded and emergent wetlands and flooded rice fields mostly occur, notwithstanding the Butte Sink wherein riparian wetlands consisting of willow *Salix* sp., California Sycamore *Platanus recemosa*, Buttonbush *Cephalanthus occidentalis* and other woody and herbaceous species exist (Gilmer *et al.* 1982; Heitmeyer *et al.* 1989; Eadie *et al.* 2008; Elphick *et al.* 2010). In Central U.S., Mallard use Gulf coastal and interior wetlands, cattle ponds, irrigation and flood-control reservoirs, playa lakes, seasonal wetlands, riparian and flooded forest wetlands, rivers and irrigation canals, plus flooded and dry agricultural lands including grain and legume crops within their geographic ranges from the Gulf Coast to southern Canada (Jorde *et al.* 1984; Chabreck *et al.* 1989; Miller *et al.* 2000; Link *et al.* 2011). In the Atlantic Flyway, Mallard use coastal and inland freshwater emergent marshes and managed wetlands developed from 18th century rice fields (Gordon *et al.* 1989, 1998). Perhaps most intriguing is the winter residency of some Mallard along the sandbar flats of the Missouri River in North Dakota, where these birds tolerate frequent inhospitable winter conditions while largely subsisting on Rainbow Smelt *Osmerus mordax* (Olsen & Cox, Jr. 2003; Olsen *et al.* 2011).

The MAV is considered the ancestral wintering grounds of North American Mallard (Nichols *et al.* 1983; Reinecke *et al.* 1989; Heitmeyer 2006). Nichols *et al.* (1983) examined winter distributions of Mallard and found support for the flexible homing hypothesis, given that Mallard wintered farther south in United States during wetter and colder winters (also see Green & Krementz 2008). Mallard typically migrate in autumn from latitudes of central Missouri after cumulative days of temperatures of ≤ 0°C, snow cover and ice conditions (*i.e.* weather severity index (WSI) of ≥ 8; Schummer *et al.* 2010). A quadratic and cumulative WSI model explained ≥ 40% of the variation in changes in relative abundance of Mallard and other dabbling ducks in Missouri during autumns–winters 1995–2005 (Schummer *et al.* 2010, 2014).

Recent capture-recapture results suggest similar patterns in Europe (Dalby 2013). Interestingly, satellite-marked Mallard in the Mississippi Flyway (Krementz *et al.* 2012) revealed patterns of incremental migrations similar to those described by Bellrose (1980).

Mulhern *et al.* (1985) investigated use and selection of wetlands by Mallard broods in Saskatchewan and found that broods used structurally different wetlands, but use was in proportion to availability of wetland types and thus not selective. How this apparent plastic habitat use by brooding ducks may ramify into habitat use subsequently during autumn and winter unearths interesting questions: 1) What drives individuals to seek and use diverse habitats? 2) What are survival and fitness outcomes related to these decisions? 3) What non-breeding habitat complexes are associated with greatest survival rates of individuals? 4) Where do these birds breed, and what are their reproductive outcomes? For example, do more competitive or fit Mallards occupy the MAV, the supposed region of greatest habitat quality for the species (Nichols *et al.* 1983), whereas other Mallard distribute to other regions? Alternatively, perhaps the regions occupied have little influence on fitness prospects, so long as adequate food, freshwater and potential mates are available. As previously mentioned, evidence exists that habitat complexes used by the greatest densities of Mallard and those individuals with greatest winter survival rates in the MAV differ in habitat composition (Pearse *et al.* 2012; Lancaster 2013; Kaminski & Davis 2014). Drivers of differential habitat use are not always clear but are likely related to foraging, weather, disturbance or a combination of these and other factors related to survival during winter. For example and relative to 3rd and 4th order selection, Mallard used irrigation canals in Nebraska agricultural landscapes over nearby natural riverine wetlands during harsh winters because canals were climatically more suitable than other habitats (Jorde *et al.* 1984). Additionally, Mallard may exercise trade-offs by selecting habitats of perhaps lesser foraging quality but prone to fewer disturbances which contribute to greater survival. Krementz *et al.* (2012) postulated that Mallard may forego wintering in the Grand Prairie region of Arkansas to avoid this area because of intense hunting pressure.

### *Northern Pintail*

Similar to their reliance on rice in California's Sacramento Valley, ~52% of all locations ($n$ = 7,022) of radio-marked Northern Pintail females were in rice habitats, which included active (18% use) and fallow rice fields (34% use) along the coast of Texas (Anderson & Ballard 2006). Many radio-marked female pintail that were located > 64 km from the Texas rice prairies flew to rice field habitats at some point during winter, which demonstrated the importance of flooded ricelands to pintail in this region (Anderson & Ballard 2006). In Louisiana, Cox, Jr. and Afton (1997) found extensive use of sanctuaries by radio-tagged Northern Pintail during hunting seasons, but less so before and after legal waterfowl seasons. Female pintail used flooded rice and fallow fields nocturnally where combined these habitats accounted for 68–93% of nocturnal use by the birds (Cox, Jr. & Afton 1997).

In California, Fleskes *et al.* (2007) attributed greater survival of Northern Pintail to increased area of flooded rice habitats. Other landscape factors important to pintail survival, such as the size and management of sanctuaries, types of feeding habitats (*e.g.* rice, wetlands) and the juxtaposition of these, may also have been important (Fleskes *et al.* 2007). Nonetheless, contemporary (1998–2000) survival estimates (87–93%) of adult female Northern Pintail in the Suisun Marsh and Sacramento and San Joaquin Valleys were greater than in any other region of North America (Fleskes *et al.* 2007). Clearly, sanctuaries adjacent to rice and other agricultural habitats are critical to survival and habitat use by Northern Pintail throughout their wintering range (Cox, Jr. & Afton 1997; Fleskes *et al.* 2007).

### *Wood Duck*

The North American Wood Duck is the only *Aix* species in the Nearctic (Birds of North and Middle America Check list; http://checklist.aou.org/). Wood Duck are also unique among North American waterfowl, because they are the only species with migratory and non-migratory populations (Baldassarre 2014). Wood Duck have been widely studied in North America since their near extirpation in the early 20th century (Bellrose & Holm 1994). Migration routes of Wood Duck are not well defined, given the substantial overlap in breeding and winter ranges (Baldassarre 2014). Given their broad occupancy of geographic areas, Wood Duck use diverse freshwater wetlands, although they avoid brackish and marine systems (Bellrose & Holm 1994; Baldassarre 2014). Despite being a forested wetland specialist, wherein Wood Duck forage on red oak *Quercus* sp. acorns and aquatic invertebrates (Heitmeyer *et al.* 2005; Foth *et al.* in press), Wood Duck also use flooded croplands where they forage on waste agricultural seeds (Delnicki & Reinecke 1986; Bellrose & Holm 1994; Barras *et al.* 1996; Kaminski *et al.* 2003). Much of the non-breeding information about Wood Duck is derived from eastern populations and birds using the MAV and southern Atlantic Flyway (Arner & Hepp 1989; Reinecke *et al.* 1989; Peterson 2014), but much remains to be learned about non-breeding Wood Duck use and selection of unique habitats in regions such as the Central Valley of California and even xeric environments in Nevada that lack traditional expansive bottomland hardwood forests (Baldassarre 2014).

## Diving Ducks

Ducks that are among the more ecologically pelagic have historically used estuarine or freshwater systems, usually along coastlines, shorelines of lakes and major rivers (Bellrose 1980). The significance to diving ducks *Aythya* sp. of myriad bays of North America, including Chesapeake and San Francisco Bays, has been recognised for centuries (Audubon 1840; Haramis 1991a,b; Perry *et al.* 2007). Unfortunately, these systems are often plagued by anthropogenic effects of shoreline development, boat traffic, increased sediments and nutrients and other factors (Perry *et al.* 2007; Lovvorn *et al.* 2013). Knowledge of niche overlap and "carrying capacity" of habitats by these ducks is necessary to understand relations between birds and potential invertebrate or other prey (Lovvorn *et al.* 2013).

Diving ducks wintering in Chesapeake Bay from 1950–1995 comprised 23% of Atlantic Flyway and 9% of North American populations of these ducks (Perry & Deller 1995; Perry *et al.* 2007). Some species wintering in Chesapeake Bay have been more adversely affected than others. For example, Redhead and Canvasback that feed on submerged aquatic vegetation (SAV), seeds and tubers have been impacted more than species that forage in slightly deeper water on invertebrates, particularly Lesser Scaup (Perry *et al.* 2007). Increased nutrients and sedimentation have lessened SAV in shallower reaches of Chesapeake Bay (Perry *et al.* 2007). Moreover, recently expanding hypoxic zones may be negatively impacting sessile prey of diving ducks (Perry *et al.* 2007) and have been linked to decreased body mass and survival in Canvasback (Haramis *et al.* 1986).

Pollutants and invasive species are thought to be especially problematic for diving ducks such as scaup and Canvasback (Lovvorn *et al.* 2013). In San Francisco Bay, Hothem *et al.* (1998) found that mercury and selenium levels in late winter had accumulated in scaup and Canvasback to levels that impair reproduction in game-farm Mallard (Heinz *et al.* 1989). Invasive species, such as Asian Clam *Potamocorbula amurensis*, which has displaced the former bivalve prey community (*e.g. Macoma balthica*), are considered a second primary concern for diving ducks in the Bay (Richman & Lovvorn 2004; Lovvorn *et al.* 2013). Asian Clams may harbour greater levels of selenium than other bivalve species (Richman & Lovvorn 2004), which could be especially problematic to Lesser and Greater Scaup as they comprised as much as 43–47% of all waterfowl in the Bay. Richman and Lovvorn (2004) collected Lesser Scaup in winters 1998–2000 and found that 98% of clams consumed by scaup were Asian Clams. Asian Clams apparently provide scaup with a profitable food source, because they mostly are distributed in the top 5 cm of sediments where scaup intake rates are greatest (Richman & Lovvorn 2004). Additionally, Lesser and Greater Scaup and Surf Scoter *Melanitta perspicillata* wintering in San Francisco Bay had decreased body mass and fat and increased foraging effort, causing them to disperse from upon food limitation. There also was substantial niche overlap and opportunistic use of dominant prey species by these ducks (Lovvorn *et al.* 2013). Lovvorn *et al.* (2013) concluded that scaup and scoter did not exploit a substantial fraction of food above local profitability thresholds before abandoning the habitat, and encouraged future research to better understand thresholds of energetic profitability for diving ducks.

Despite vast size and dynamics of San Francisco Bay, adjacent habitats in the region provide vital resources for some species using the Bay. Specifically, estuarine intertidal and subtidal mudflats and salt ponds provide additional food and water for diving ducks (Dias 2009; Brand *et al.* 2014). Brand *et al.* (2014) found that diked salt ponds, salt pans and managed seasonal wetlands in South San Francisco Bay collectively provided enough food energy to sustain 79% of the energy and nutrients required by diving ducks when birds were at maximum numbers, and basically 100% of the nutrients when average bird abundances prevailed. Managed ponds serve as important roosting and foraging habitats in this region. Ponds that intake, circulate or discharge water directly to or from the Bay or adjacent sloughs supported > 95% of the diving duck abundance (Brand *et al.* 2014). However, greater bird and invertebrate abundances and prey energy density occurred in meso-haline (*i.e.* 5–30 ppt) rather than low-hypersaline (*i.e.* 31–80 ppt) circulation ponds (Brand *et al.* 2014). Ruddy Duck *Oxyura jamaicensis* exercise dietary flexibility in these same wetland complexes, feeding on amphipods *Amphipoda* sp. or polychaetes *Polydor*a sp. depending on prey occurrence or abundance among different wetland types (Takekawa *et al.* 2009; Brand *et al.* 2014). Thus, similar to identifying important habitat complexes for Mallard or other dabbling ducks (Pearse *et al.* 2012; Lancaster 2013), maintaining diverse foraging wetlands in ecosystems like San Francisco Bay is imperative for supporting waterfowl and other wetland dependent birds using this system (Brand *et al.* 2014).

A primary difference between historical and contemporary habitat use for some diving ducks, such as Ring-necked Duck in the U.S., has been a shift away from traditional winter habitats to open-water lakes because of a proliferation of invasive plants such as Hydrilla *Hydrilla verticillata* and other species that form dense floating mats (Johnson & Montalbano 1984; Roy *et al.* 2013). Some of the greatest wintering concentrations of Ring-necked Duck may occur in managed impoundments of coastal and inland Louisiana (Roy *et al.* 2013). Ring-necked Duck use small marshes adjacent to open water, whereas Canvasback, Redhead and scaup typically use open-water areas only (Korschgen 1989; Roy *et al.* 2013). Elsewhere herein, Stafford *et al.* (2014) provided a detailed account of scaup habitat use during late winter and spring migration. Diverse coastal and interior wetlands of south-central Louisiana are critical to diving ducks such as Redhead and Canvasback (Hohman & Rave 1990; Hohman *et al.* 1990). Canvasback in the Mississippi River Delta and at Catahoula Lake in Louisiana, both important wintering areas to these species (Hohman *et al.* 1990), consumed about 97% plant matter at each site, with below-ground plant biomass composing 94% aggregate dry mass (Hohman & Rave 1990). Mudflats with tubers or water that permitted Canvasback to tip-up and feed were important components of used habitats (Hohman & Rave 1990). Similar to plant-eating Canvasback, the importance of Shoal Grass *Halodule wrightii* to Redhead and several avian guilds has long been mentioned (Cornelius 1977; Michot *et al.* 2008). Redhead wintering in the Chandeleur Sound of Louisiana and Laguna Madre, Texas consumed as much as 74% dry mass of shoalgrass (Michot *et al.* 2008). Conserving *Halodule* beds arguably is the most critical conservation priority within the winter range of Redheads, particularly given that most of the North American population of the species winters along coastal habitats of Texas and Louisiana (Michot *et al.* 2008).

## Sea ducks

### *North America*

There are 15 species of North American sea ducks (Tribe: Mergini) and arguably they are the least understood taxa of waterfowl (Bellrose 1980; Goudie *et al.* 1994; Silverman *et al.* 2013). Evidence suggests that 10 of these species are in decline, including eight of 12 species that winter off the Atlantic coast of North America, a primary wintering area for this tribe (Sea Duck Joint Venture 2004; Zipkin *et al.* 2010). Eleven species of sea ducks commonly winter in Pacific coastal regions, nine of which commonly occur in the Puget Sound of Washington state (Faulkner 2013). Sea duck declines are occurring concomitantly with uncertainty about their habitat preferences (Zipkin *et al.* 2010). Shoreline development and associated pollution and climate change are potential negative influences on sea ducks in North America (Zipkin *et al.* 2010). Recent proposals for wind turbines along the Atlantic coast and threats from offshore energy development will also challenge sea ducks, so further understanding of habitat selection by these ducks is imperative (Zipkin *et al.* 2010).

Spatial distribution of sea ducks is generally determined by winter weather conditions and habitat diversity (Zipkin *et al.* 2010). At greater spatial winter ranges, food availability, local environmental conditions, habitat suitability, ocean depths and water temperatures influence sea ducks' use of habitats (Lewis *et al.* 2008; Zipkin *et al.* 2010; Dickson 2012). Northern seas are hostile during winter, with below freezing temperatures, wind, ice and limited daylight because the sun is below the horizon for two months (Systad *et al.* 2000). Sea ducks, however, remain in these rigorous environments during winter and forage on molluscs, echinoderms, crustaceans and other invertebrates. These foods are depauperate in energy density, so sea ducks must forage voraciously to maintain positive energy balances (Systad *et al.* 2000).

Surf Scoter *Melanitta perspicillata* and White-winged Scoter *M. deglandi* in the Pacific Flyway use soft-bottom habitats and forage on bivalves (Bourne 1984; Richman & Lovvorn 2003; Lewis *et al.* 2008). Scoters encounter considerable variation in clam densities and potentially face an exhaustible food supply (Lewis *et al.* 2008). However, Lewis *et al.* (2008) found that scoters in Baynes Sound (British Columbia) did not switch winter prey or move extensively to foraging sites, suggesting clam density was relatively high there (Kirk *et al.* 2007).

Sea ducks in the eastern U.S. have been monitored by the Atlantic Flyway Sea Duck Survey (AFSDS) in at least nine bays and sounds off of the Atlantic coast to quantify winter distributions and population indices (Migratory Bird Data Center 2009; Zipkin *et al.* 2010). Zipkin *et al.* (2010) modelled effects of bottom depths, monthly averages of sea surface temperature, and ocean floor topography for five species of wintering sea ducks. The North Atlantic Oscillation (NAO; *i.e.* fluctuation in sea surface pressure across the northern Atlantic Ocean between areas of high (Azores High) and low (Icelandic Low) pressure: Ottersen *et al.* 2001; Stenseth *et al.* 2002; Hurrell *et al.* 2003; Zipkin *et al.* 2010) was the only environmental covariate that had a significant influence on all five species; its effect was negative for the three scoter species and positive for Common Eider and Long-tailed Duck *Clangula hyemalis* (Zipkin *et al.* 2010). These results suggest that climatic conditions along the Atlantic coast during migration and winter may have direct or indirect influences on sea duck distributions, perhaps as prey are re-distributed (Zipkin *et al.* 2010). Scoters predominated inshore during cold, snowy winters and Common Eider and Long-tailed Duck were more abundant inshore during wet, mild winters (Zipkin *et al.* 2010). Sea surface temperature (SST) negatively affected Long-tailed Duck and White-winged Scoter abundance but positively affected Common Eider, although there was some interaction of effects between NAO and SST on birds' habitat distribution. Overall, sea ducks may respond to a combination of local habitat conditions and broader-scale weather patterns (Zipkin *et al.* 2010). Collectively, scoters used flatter bottom sites, which seemed consistent with knowledge that Black Scoter *Melanitta americana*, Surf Scoter and White-winged Scoter preferred sandier basins along the Atlantic shoreline (Stott & Olson 1973; Zipkin *et al.* 2010). In contrast, Common Eider used rugged substrates, but Long-tailed Duck have not yet been linked to bottom substrates (Perry *et al.* 2007; Zipkin *et al.* 2010).

Other important habitats for non-breeding sea ducks in central and eastern North America include the Great Lakes and Chesapeake Bay (Schummer *et al.* 2008). Mixed species of Bufflehead *Bucephala albeola*, Common Goldeneye and Long-tailed Duck use inshore areas of Lake Ontario and forage on energy-dense *Amphipoda* and larvae of *Chironomidae*, both abundant in the shallow-water zone near shore (Schummer *et al.* 2008). Despite concentrated mixed flocks of ducks, Schummer *et al.* (2008) did not detect declining abundances of macroinvertebrates during winter. They concluded that exploitative competition was likely not occurring and interference competition appeared below thresholds that would cause birds to spatially segregate. Overall, winter forage did not appear to limit habitat use of these species in Lake Ontario during winter (Schummer *et al.* 2008).

Chesapeake Bay is considered one of the most important areas for several species of scoters and Long-tailed Duck (Sea Duck Joint Venture 2004; Ross *et al.* 2009), but little is known about the birds' use of the system. Surf Scoter *M. perspicillata* is thought to forage preferentially in subtidal, sandy soft sediment habitats > 6 m deep (Ross *et al.* 2009), but will also use hard-substrates (Lewis *et al.* 2007; Perry *et al.* 2007). Long-tailed Duck in the upper Chesapeake Bay primarily consume bivalves (Perry *et al.* 2007), likely procuring food from soft-sediment areas (Žydelis & Ruskete 2005; Ross *et al.* 2009). Ross *et al.* (2009) suggested that limited availability of hard substrate bottom in Chesapeake Bay might dictate habitat use patterns among these sea ducks in the upper Chesapeake compared to other regions. Further concerns are linked to declining water quality since the 1960s in the lower region of Chesapeake Bay (Ross *et al.* 2009). Excessive sedimentation and nutrient loading have caused eutrophication and oxygen depletion, negatively affecting portions of the Bay's substrate, and are linked to dramatic declines in seagrass beds (Chesapeake Bay Program 2007; Ross *et al.* 2009). These consequences are problematic because seagrasses supply important substrates for bivalves compared to bare ground under the Bay (Peterson 1982; Peterson *et al.* 1984; Ross *et al.* 2009).

### *Europe*

Recent count data indicate that most European sea duck populations, with the exception of Common Goldeneye, are now in decline (Hearn & Skov 2011; Skov *et al.* 2011). Common Goldeneye winter extensively in freshwater habitats along coastlines, whereas other sea ducks tend to have an offshore distribution. The Baltic Sea is the key wintering area for most European sea ducks, and it is a region of major concern. Recent surveys indicate that Long-tailed Ducks, Velvet Scoter and Steller's Eider have declined by 65%, 55% and 66%, respectively, with declines in Common Eider (51%), Common Scoter (47%), Red-breasted Merganser *Mergus serrator* (42%) and Greater Scaup (26%) also recorded (Skov *et al.* 2011). Declines have similarly been reported in other European countries, notably in Britain and the Netherlands, which are also important wintering grounds for European sea duck populations. Generally, wintering sea ducks aggregate in shallow coastal waters or over offshore banks where they can dive for food on the sea floor. In winter, > 90% of sea ducks use areas amounting to < 5 % of the Baltic Sea (Bellebaum *et al.* 2012), where they forage primarily on Blue Mussel *Mytilus edulis*.

Ecosystem changes that have a negative effect on habitat and food resources during the non-breeding season (*e.g.* extraction of sand and gravel, dredging of shipping channels or coastal development), are potentially the most important explanation for the decline in arctic-breeding sea duck populations (Skov *et al.* 2011). Moreover, shipping and offshore wind farms may permanently displace sea ducks from favoured feeding grounds (Petersen *et al.* 2006; Skov *et al.* 2011). Among sea duck species, the Long-tailed Duck is particularly sensitive to wind farms (Petersen *et al.* 2006), and plans for offshore wind farm construction exist in all Baltic countries. Traffic along the major shipping routes (which cross or pass close to Long-tailed Ducks wintering sites) is also predicted to increase (Skov *et al.* 2011). Oil illegally discharged from ships continues to kill tens of thousands of birds each year, despite enforcement of international regulations (Larsson & Tydén 2005; Skov *et al.* 2011; Brusendorff *et al.* 2013), and other hazardous chemicals are suspected of having a negative impact on Baltic wildlife (including sea ducks) when birds ingest bivalves or organisms that filter polluted sea water (*e.g.* Pilarczyk *et al.* 2012; *cf.* Skov *et al.* 2011). Additionally, sea duck food resources in the Baltic Sea have changed substantially in recent decades concomitantly with nutrient loading. Increase of nutrient loads after 1950 might explain rising bivalve biomass in shallow waters, which in turn may have stimulated sea duck population growth. But decreases in nutrient loads (nitrogen and phosphorous) have occurred in some coastal regions since the 1990s, whereas nutrient levels remain high in other parts of the Baltic Sea. Declines in nutrient loads along the coastline and subsequent effects on sea duck food quality need further investigation. Nevertheless, Skov *et al.* (2011) stressed the importance of eutrophication in spatio-temporal variability in food supply for and abundance of waterbirds in the Baltic Sea, with control of eutrophication being a plausible reason for the decrease of several benthic species in Danish waters.

Phytoplankton composition also has changed in the Baltic, perhaps through the increase in water temperatures in recent decades or overfishing leading to a decrease in food quality for filter-feeding bivalve mussels. In addition, in warmer waters mussels metabolise their own reserves during winter instead of hibernating, which could decrease the quality of mussels for bivalve feeders (Waldeck & Larson 2013). Lastly, overexploitation by commercial mussel fisheries (*e.g.* in the Wadden Sea) may cause food shortages for bivalve feeding species such as Common Eiders (Skov *et al.* 2011).

Concomitant with warming temperatures of the Baltic Sea, ice coverage has decreased and permitted access to new wintering areas for waterfowl. Common Goldeneye and some *Aythya* species are shifting northward in their wintering distribution in the Baltic Sea (Skov *et al.* 2011; Lehikoinen *et al.* 2013). The limited degree of northward shift in the distribution of seaduck feeding offshore suggests reduced food availability in the northern Baltic area, which is now partly ice-free in winter. Nevertheless, populations of some species including Common Eider have relocated to the southwest Baltic Sea from previous wintering quarters in northwest Denmark. Lastly, European sea duck populations also may be directly or indirectly affected by commercial fishing and the use of gillnets for fishing (Žydelis *et al.* 2009).

## Geese

### *Geese and agriculture*

As for ducks, habitat modifications influence distribution, movement and resource exploitation in geese. Geese are generally more adept at exploiting farm crops than most duck species (Owen 1980), so their autumn and winter habitat use is largely driven by and has changed markedly in response to variations in farming practices, both in North America and Europe, during the 20th and 21st centuries. For example, Pacific Flyway Greater White-fronted Geese commonly stage in the SONEC, and then migrate and winter in the Sacramento and San Joaquin Valleys (Ely 1992; Ackerman *et al.* 2006; Ely & Raveling 2011). Approximately 80% of foraging flocks of White-fronted Geese used harvested barley, wheat or oat fields from early September to mid-October in SONEC, 1979–1982, then switched to potato fields by mid-October–late November of those years (Frederick *et al.* 1992; Ely & Raveling 2011). When White-fronted Geese migrated to the Sacramento Valley in autumn and winter, they primarily used complexes of rice field habitats (Ely & Raveling 2011). After White-fronted Geese departed the Sacramento Valley for the San Joaquin Valley, green forage, waste corn and other grain and vegetable crops were available to the geese, but birds disproportionately used corn relative to its availability (Ely & Raveling 2011). The future of Greater White-fronted Geese in the San Joaquin Valley is uncertain because corn acreage declined there by 20%, largely because of urbanisation (Ackerman *et al.* 2006; Ely & Raveling 2011). Changes in agricultural practices and crops produced are commodity-market driven and largely beyond the control of wildlife biologists, thus challenging to conservation planning (Ely & Raveling 2011; Skalos 2012; Petrie *et al.* 2014).

Another striking example of dynamic habitat use by geese within agricultural landscapes comes from the North American Snow Geese and Ross' Geese *Chen rossii* (Ankney 1996; Abraham *et al.* 2005). White goose use of waste grain is well documented in the literature (Alisauskas *et al.* 1988; Ankney 1996; Alisauskas 1998; Abraham *et al.* 2005). Recent research has sought to identify winter origins of white geese migrating through Nebraska's Rainwater Basin, a region of continental significance to autumn and spring migrating waterfowl and Sandhill Crane *Grus Canadensis* (Krapu *et al.* 1984; Alisauskas & Ankney 1992; Alisauskas 2002; Stafford *et al.* 2014). Henaux *et al.* (2012) used stable isotope analysis and found flexibility in diets and regional landscape use by Snow Geese. They determined origins of wintering Snow Geese harvested in the Rainwater Basin as follows: Louisiana (53% and 9% in 2007 and 2008, respectively), Texas Gulf Coast (38% and 89%, respectively), Arkansas (9% and 2%, respectively). However, no birds from the Playa Lakes region were detected. Beyond annual variability in their winter origins, differences in diet also helped to characterise their winter habitat use. Snow Geese relied on rice and wheat fields ($C_3$ plants isotopic signature) as well as corn and grain sorghum ($C_4$ plants). Geese collected from Texas and Louisiana were generally characterised by using estuarine and marsh habitats *versus* uplands typical of Arkansas and playa eco-regions (Alisauskas & Hobson 1993).

General plasticity of North American white geese in exploiting agricultural and marsh habitats (Bateman *et al.* 1988; Alisauskas 1998; Jefferies *et al.* 2004) creates complex challenges in arresting the growth of overabundant populations in the 21st century (Batt 1997; Jefferies *et al.* 2004; Abraham *et al.* 2005). However, dwindling rice acreage in Texas may influence white goose population levels. For example, rice acreage was ~203,152 ha and white geese numbered > 1.2 million in 1979; whereas ~378,000 geese were counted and only > 54,000 ha of rice existed in Texas in 2013 (K. Hartke, Texas Parks and Wildlife, unpubl. data). The contemporary estimate of rice acreage is the lowest ever for Texas since records originated *ca.* 1948 (K. Hartke, Texas Parks and Wildlife, unpubl. data).

Similarly, contemporary estimates of geese wintering in the Western Palearctic are 4.8 million, up from 3.3 million in 1993 (Fox *et al.* 2010). Most species exhibit signs of exponential increase, whereas others (*e.g.* the Greenland White-fronted Goose *Anser albifrons flavirostris*, Red-breasted Goose *Branta ruficollis* and Dark-bellied Brent Goose *Branta bernicla*) have declined in recent years (Fox *et al.* 2010). Although reduced hunting pressure on geese in some regions probably played an important role, increases in most species of European geese have likely resulted from exploitation of grains and root and grass crops, similar to patterns in North America (Abraham *et al.* 2005; Fox *et al.* 2010). Since the 1950s, wild geese wintering in the western Palearctic have partially or completely switched from feeding on natural vegetation to managed pastures and agricultural croplands (Madsen 1998; Jensen *et al.* 2008; Hake *et al.* 2010). Agricultural producers in Europe have been concerned with losses of wheat and oilseed as goose and swan populations have increased (Dirksen & Beekman 1991; Rees *et al.* 1997). Several measures have attempted to deter geese from crops, including providing supplemental feed in accommodation fields to influence movements of and use by geese, scaring of birds, fencing habitats and adjusting farming strategies, such as growing barley varieties that mature and are harvested before varieties used previously (Hake *et al.* 2010).

### *Black Brant and estuarine-marine systems*

Besides agricultural lands, estuarine and marine wetland systems are critical to many waterfowl, including Black Brant in North America (named Brent Goose in Europe). Important autumn staging areas for brant include shallow marine waters along shorelines, within lagoons or behind barrier beaches (Shaughnessy *et al.* 2012; Lewis *et al.* 2013). Some of the important habitats for the nine-month non-breeding period of brant include the Northeast Pacific United States, the lagoons along the west coast of Baja California, areas of Mexico and Atlantic coastal habitats (Smith *et al.* 1985; Lewis *et al.* 2013, Martínez Cedillo *et al.* 2013). Pacific Black Brant solely use natural habitats during winter and avoid agricultural lands (Ward *et al.* 2005; Lewis *et al.* 2013). As mentioned, the unifying food resource for Holarctic brant is eelgrass (Moore *et al.* 2004; Moore & Black 2006; Shaughnessy *et al.* 2012; Lewis *et al.* 2013). Macrogreen Algae *Ulva* sp. beds also serve as important food in coastal areas in the Atlantic Flyway (Lewis *et al.* 2013). Brant exhibit different foraging strategies in Atlantic coastal states of New York, New Jersey and Virginia, where brant select eelgrass, cordgrass *Spartina* sp. or exploit grasses and clover in upland habitats (Smith *et al.* 1985). Smith *et al.* (1985) attributed diet switching by brant from eelgrass to other foods because of eelgrass declines. However, brant foraged on cultivated grass and clovers in New York, despite an increasing trend in availability of SAV in the state. They attributed differential feeding strategies among regions to the birds' winter philopatry and social organisation.

Brant have been negatively affected by loss of eelgrass habitats in the North American Atlantic Flyway and Europe (Vickery *et al.* 1995; Ganter *et al.* 1997; Ward *et al.* 2005; Shaughnessy *et al.* 2012). Brant in those regions use eelgrass where available, but birds also exploit salt marsh habitat. Moreover, European birds have moved inland to use golf courses and pastures with cattle (Vickery *et al.* 1995; Ganter *et al.* 1997; Ward *et al.* 2005; Shaughnessy *et al.* 2012). Lovvorn & Baldwin (1996) recognised the value of habitat complexes for wintering brant in Western Europe that include intertidal flats, bays and other permanent wetlands that provide sea grasses, as well as nearby farmlands containing waste grains and natural seeds. This complex of suitable habitats allow brant to move and forage among them and thereby enhance their survival (Lovvorn & Baldwin 1996). However, synergistic effects of climate change, possible negative effects on sea level rise and declining eelgrass communities are emerging concerns for waterfowl ecologists conserving brant (Shaughnessy *et al.* 2012).

## Swans

### *Migratory swans*

Of the five swan species and subspecies in the northern hemisphere, the Tundra Swan (a.k.a. Whistling Swan) *C. c. columbianus* and Trumpeter Swan of North America and the Bewick's Swan *C. c. bewickii* (conspecific with the Tundra Swan) and Whooper Swan *C. cygnus* in Eurasia are all migratory, whereas the Mute Swan *C. olor* is relatively sedentary in its native Europe and in North America where it has colonised (*e.g.* Petrie & Francis 2003). Trumpeter Swans were widespread in North America prior to 1900 (Rogers & Hammer 1998; Engelhardt *et al.* 2000), but hunting caused their numbers to drop nearly to extinction by the early 20th century, and use of established migration routes waned (Gale *et al.* 1987; Mitchell & Eichholz 2010). Legal protection from persecution (since the 1918 Migratory Bird Treaty) and more recent conservation measures (*e.g.* habitat protection and reintroduction programmes) saw Trumpeter Swan numbers recover to ~16,000 birds by 1990, and > 34,000 free-ranging swans were estimated in 2005 (Moser 2006; Mitchell & Eichholz 2010). Whooper Swan numbers have also increased in Europe in recent decades (Wetlands International 2014), and the Tundra Swan – the most numerous and widely distributed of North American swans – is likewise increasing. Indeed, agricultural foraging opportunities are thought to have contributed to a near doubling of Tundra Swan numbers (to > 200,000 birds) between 1955–1989, leading to regulated hunting of the species in some states (Serie & Bartonek 1991). In contrast, although the Northwest European Bewick's Swan population similarly rose from ~16,000 birds in the mid-1980s to a peak of ~29,000 individuals in the mid-1990s, its numbers are now in decline (Rees & Beekman 2010), with several poor breeding seasons in recent years probably a major contributing factor.

The Eastern Population of Tundra Swans, which breeds across northern Canada and north of the Brooks Range in Alaska, migrates to the U.S. eastern seaboard (allocating about half their time between boreal forest and northern prairie-Great Lakes habitats during autumn migration; Weaver 2013), whereas the Western Population, which breeds in coastal regions of Alaska south of the Brooks Range, migrates to western North America to winter mainly on the Pacific coast from Vancouver Island to central California, and the inland valleys of California (Bellrose 1980; Ely *et al.* 2014). The Northwest European Bewick's Swan population also migrates along a well-defined corridor, from breeding grounds in the Russian arctic along the arctic coast and across Karelia to autumn staging sites on the Baltic (particular Estonian wetlands) and wintering grounds in northwest Europe. Whooper Swans are thought to migrate on a broader front (Garðarsson 1991; Matthiasson 1991), but like the arctic-nesting swans they show strong fidelity to staging and wintering sites (Bellrose 1980; Black & Rees 1984; Rees 1987).

Historically, migratory swans fed on SAV during autumn and winter, often reflecting regional and seasonal variation in availability and dietary requirements. For Tundra Swans, this included Arrowhead *Sagittaria* sp., Sago Pondweed *Potamogeton pectinatus* and Wild Celery *Vallisneria americana* (Bellrose 1980), with Bewick's Swans also favouring pondweeds (*Potamogeton pectinatus* and *P. perfoliatus*) along with hornworts *Ceratophyllum* sp., watermilfoil *Myriophyllum* sp., stoneworts *Chara* sp. and other emergent vegetation (Rees 2006). However, wetland drainage and intensification of farming (including increased use of fertiliser on grasslands and more extensive planting of arable crops) has resulted in a large-scale movement of swans from wetland habitats to agricultural land. In Europe, Whooper Swans were recorded feeding on cereals and potatoes as early as the 19th century, but changes in agriculture saw an increase in their use of arable habitats during the second half of the 20th century (Kear 1963; Laubek *et al.* 1999). More recently, Tundra Swans were first observed in grain fields in the mid 1960s (Nagel 1965; Tate & Tate 1966; Munro 1981), and Bewick's Swans have been utilising arable habitats since the early 1970s (review in Rees 2006). Trumpeter Swans typically use freshwater marshes, ponds, lakes, rivers and brackish estuaries with abundant pondweed (Gale *et al.* 1987; LaMontagne *et al.* 2003; Mitchell & Eichholz 2010), but also forage on arable land in winter and early spring (Babineau 2004; Mitchell & Eichholz 2010), where they avoid soybean and prefer winter wheat and corn (Varner 2008). In the mid-west U.S., swans use reclaimed surface mine wetlands close to agricultural fields, which rarely freeze and are relatively undisturbed compared to reservoirs (Varner 2008; Mitchell & Eichholz 2010). The drivers of swan exploitation of arable lands remain unclear; however, historic and novel food availability, nutrition and foraging efficiency in croplands may be influences (Rees 2006). Several studies have described seasonal variation in the swans use of farmland, with birds generally moving from harvest waste (*e.g.* cereal stubbles, potatoes and sugar beet) to growing cereals (*e.g.* winter wheat) and then to pasture as the winter progresses, which has been attributed to a combination of food availability and changes in dietary requirements (*e.g.* Laubek 1995; Rees *et al.* 1997). Weaver (2013), studying habitat use by 63 satellite-tagged Tundra Swans, found seasonal differences in habitat selection. Tundra Swans selected open water over wetlands in autumn, but agriculture was used substantially less during autumn migration (despite representing 45% and 80% of Tundra Swan habitats in the Great Lakes and Northern Prairies, respectively, at this time) than in winter, when swans selected agriculture lands, and wetlands were used less than their availability. Weaver (2013) concluded that if adequate aquatic habitats were available, swans may not have made forays to agricultural fields, although agricultural seeds provided alternative foods of similar energy value (Kaminski *et al.* 2003), and recommended that wetland conservationists interested in managing non-breeding Tundra Swans should conserve and restore wetlands within agricultural landscapes < 8 km of known roosts and aim to protect open water habitats, especially those containing SAVs. Detailed studies of Bewick's Swan feeding ecology have also illustrated the importance of aquatic habitats for swans arriving in autumn, with swans feeding on below-ground Fennel Pondweed tubers at the Lauwersmeer, Netherlands, preferably in shallow waters and sandy sediments rather than in areas of deeper water, likely reflecting increased effort and energy costs (*e.g.* up-ending as opposed to head-dipping for food) required to feed in deeper waters or where the tubers are in clay (Nolet *et al.* 2001). Further analysis of the timing of the swans' switch from feeding on pondweed tubers to feeding on sugar beet in fields around the Lauwersmeer found that most swans switched habitats when the net energy gain from staying on tubers fell below that from feeding on beet alone. However, the swans would attain a substantially increased energy and total nutrient gain by feeding on both beet and tubers, and there was evidence from van Eerden (1997) that mixed exploitation of tubers and beet does occur in the Lauwersmeer area. Overall, swans seemingly switch to the beet fields long after they would first benefit from doing so due to energy gain alone (Nolet *et al.* 2002).

### *Mute Swans*

Mute Swan movements tend to be relatively localised (< 50 km radius; Birkhead & Perrins 1986), although some long-distance flights have been recorded (*e.g.* those at more northerly latitudes heading south in cold winters). They frequent a wide range of lowland wetland habitats throughout the year, including freshwater lakes, estuarine wetlands, commercial fishponds, sea lochs and shallow coastal waters, where they feed primarily on SAV, and are also commonly found on rivers and canals in urban areas where they rely on bread and other provisions from humans (Birkhead & Perrins 1986; Sears 1989; Gayet *et al.* 2011). They also use farmland, for instance moving to agricultural fields and improved grasslands during winter (Birkhead & Perrins 1986), but tend to be more widely dispersed than the migratory species (Rees *et al.* 1997). In parts of the United Kingdom, where three swan species (Bewick's, Whoopers and Mutes) coincide in winter, segregation across habitats has been recorded, with Whooper and Mute Swans predominately using permanent inland waters and improved pasture, whereas Bewick's Swans were mostly on arable land (Rees *et al.* 1997), indicating a range of habitats are important for foraging by these swan species.

On studying effects of patch size and isolation on Mute Swan habitat use in France, Gayet *et al.* (2011) found that the swans' winter distribution and occurrence on fishponds was influenced by pond structure more than surrounding landscape and other features. Specifically, fishponds drained and cultivated for grain the previous year provided crop residues utilised by the swans the following winter. Understanding habitat selection of Mute Swans is important because they are perceived as having negative influences on other waterfowl, through territorial behaviour or intensive grazing on aquatic macrophytes, sometimes within their European range but particularly where they have been introduced to North America (Conover & Kania 1994; Petrie & Francis 2003; Gayet *et al.* 2011), with a Mute Swan control programme instigated in Maryland in 2005 (Hindman & Tjaden 2014; Hindman *et al.* 2014).

## Future challenges and needs

Planning and implementing conservation strategies for waterfowl and their habitats are challenging because some species are declining or remain below long-term averages (*e.g.* Scaup, Northern Pintail American Wigeon), whereas others have become superabundant (*e.g.* Snow Goose) despite some using similar resources (*e.g.* agricultural fields used by Northern Pintail and Snow Geese) in autumn and during migration. Wiens (1989) discussed habitat quality in terms of "fitness potential", whereby habitat quality may be assessed through demographic, physiological and behavioural approaches. Nonetheless, Norris & Marra (2007) alluded to the difficulty in understanding habitat selection in migrating species, particularly in identifying spatio-temporal connectivity of individuals or populations among stages of the annual cycle. Indeed, there is strong research and conservation interest in determining the extent of migratory connectivity among birds occupying specific wintering and breeding areas (Norris & Marra 2007; Guillemain *et al.* 2014; Kaminski & Elmberg 2014). Here we consider some challenges hindering understanding of habitat use and selection by waterfowl during the non-breeding season and suggest future needs for research. We recognise there are other ecological, economic, bio-political and human dimensional considerations, but believe that addressing the following five issues will advance science and stewardship of waterfowl and their habitats in the Holarctic and worldwide.

(1) *Habitat and resource availability*. Resources available for migrating and non-breeding waterfowl are typically dynamic and unpredictable. Indeed, many migratory birds (*e.g.* Svalbard Barnacle Geese) seemingly cannot assess local resource conditions from afar and must "sample" habitats upon settling in them, though others (*e.g.* Svalbard Pink-footed Geese *Anser brachyrhyncus*) appear to use conditions at one site as an indicator of conditions that they might encounter at the next (Tombre *et al.* 2008). Habitat and other environmental dynamics may result in patchily distributed food and other resources within and across seasons, inter-annual site-specific changes in potential foraging areas (*e.g.* ploughed *versus* flooded field; 4th order selection), natural inter-annual droughts or flooding, weather that may dictate where birds winter and exploit resources, disturbance from hunting and other human-related factors, physiological and behavioural dynamics and other scenarios (Fig. 1). During winter, some species like Northern Pintail, Mallard, teal and diving ducks move inter-regionally, likely in search of suitable habitats (*sensu* Fretwell 1972; Cox, Jr. & Afton 1996; Heitmeyer 2006; Caizergues *et al.* 2011; Gourlay Larour *et al.* 2013). Interpreting true migration from movements to and fro (*i.e.* foraging flights) can be challenging (Dingle & Drake 2007) and documenting habitat selection across broad landscapes in brief intervals may be even more equivocal.

Arguably, one of the greatest current challenges waterfowl habitat researchers face relative to identifying true selection involves an inability to determine true habitat and resource availability at scales influencing biological outcomes for the birds (Kaminski

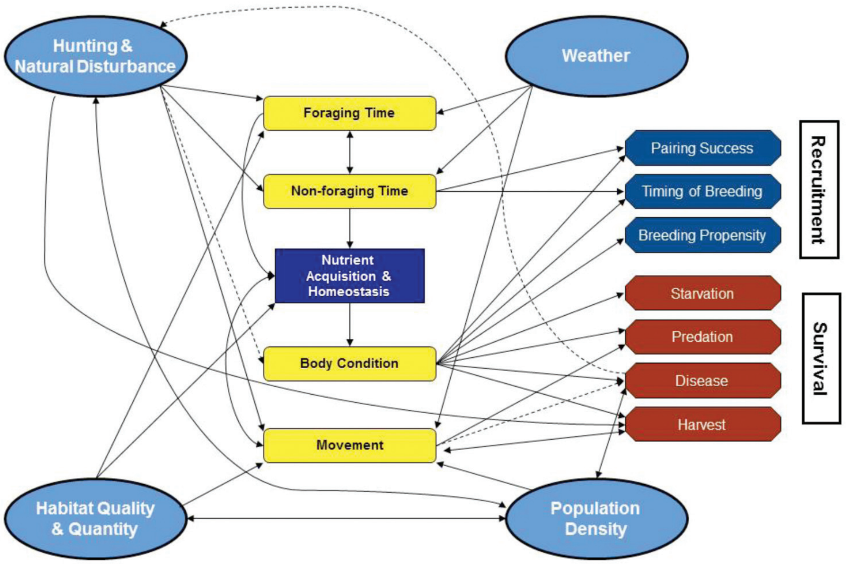

**Figure 1**. A synthesis of primary and secondary factors that influence survival and potential fitness of Holarctic waterfowl.

& Elmberg 2014). For example, non-breeding waterfowl that exploit agricultural environments (thousands of hectares of agricultural land in one region alone) may suddenly move from dry to shallowly flooded fields during autumn–winter (Reinecke *et al.* 1989). Mallard commonly feed in dry fields in southern Canada and the northern U.S. prairies, but not in the MAV where they utilise puddled fields. This typical scenario is further complicated during winters of below average temperatures; then, Mallard use dry agricultural fields in winter as wetlands freeze and foods become inaccessible. These and other scenarios create great resource variability across regions, temporal variability within regions, and basically constrain researchers' efforts to categorise and estimate available resources. We concur that recent analysis of habitat use by mid-continent Mallard (Beatty *et al.* 2013) is statistically robust, but may be ecologically tenuous because they could not estimate full availability of agricultural lands possibly accessible by Mallard. Despite broad spatial and temporal scaled information obtainable from satellite-tracked birds (Krementz *et al.* 2012; Beatty *et al.* 2013), sample sizes of marked birds are often small because of funding limitations (Lindberg & Walker 2007). This limitation constrains determining selection of habitats, because a small cohort of individuals is assumed to represent the greater population. Moreover, when making inferences of resource selection beyond one or two variables, sample sizes must be increased significantly (Lindberg & Walker 2007). Given the challenges in capturing environmental variability across vast landscapes, we suggest long-term studies (*i.e.* ≥ 5 years) should be invoked to reflect patterns of waterfowl resource selection amid environmental stochasticity.

Habitat conservation for non-breeding waterfowl is justified on the assumption that certain important habitats and intrinsic food resources are limited and thereby ramify individual and population implications (NAWMP 2012). However, to our knowledge (and as emphasised by Stafford *et al.* 2014), true resource limitation has not been demonstrated empirically by relating food or other resource abundance to biological outcomes for waterfowl. Indeed, further understanding these scenarios is required for assessing whether true resource limitation exists and is affecting individuals and populations (Neu *et al.* 1974; Johnson 2007; Stafford *et al.* 2014).

(2) *Populations important to study*. Individuals of some species (*e.g.* Mallard), are widespread in North America during autumn and winter (Bellrose 1980). Some Mallard winter along sandbars and adjacent agricultural lands along the Missouri River in North Dakota (Olsen & Cox, Jr. 2003), while others predominately occupy the southern U.S. (Nichols *et al.* 1983; Reinecke *et al.* 1989). We typically regard the former region as "breeding grounds", yet some Mallard remain there during winter. Although some resources (*e.g.* agriculture) in all these geographic regions get exploited by Mallard, basing habitat selection on a cohort of a species in one region may not reflect important resource components elsewhere in the species' range. Thus, what cohorts of birds should be studied? Comparative studies of conspecifics across geographic regions would be interesting and valuable; thus, studying non-breeding resource use and in regions with the greatest abundance of individuals of a species is a suggested approach. The genetic variability among individuals in these regions should reveal patterns of resource exploitation important to subsequent breeding success. The greater challenge and future research endeavour is to discover if population cohorts of a species that occupy ecologically disparate landscapes during non-breeding seasons contribute differently to population recruitment for the species. Conversely, analysis of bands recovered over a large geographical area have demonstrated that some population boundaries in western Europe were largely artificial (Guillemain *et al.* 2005), so that habitat selection studies should be conducted at much greater geographic scales.

(3) *Functional use of habitats*. Understanding the range of benefits that birds derive from different habitats is also a critical need. Time-budget studies have been conducted at sites across the Holarctic for decades, but new technology such as unmanned aircraft (drones) or GPS accelerometers would help to quantify the birds' activities at local and micro-habitat scales, which in turn would improve our knowledge of the functional values of habitats frequented by waterfowl.

(4) *Remoteness and difficulty in accessing habitats*. Inhospitable conditions and remoteness of habitats pose challenges to studying birds such as sea ducks (Silverman *et al.* 2013) and other arctic-nesting waterfowl. Establishing true habitat selection

among sea ducks in remote environments, especially when trying to link movements or habitat use in relation to food, is particularly problematic. Researchers hypothesise that serious challenges face wintering sea ducks, including marine (boat) traffic, wind-power development and aquaculture practices (Skov *et al.* 2011; Silverman *et al.* 2013). Despite inherent difficulties in investigating birds and habitats in marine environments, recent research has greatly advanced understanding of non-breeding ecology of sea ducks, albeit continued efforts are essential to sustain these birds (Faulkner 2013; Silverman *et al.* 2013).

(5) *Cumulative resource use.* Lastly, there exists a lack of understanding of how cumulative use of resources during the non-breeding period may influence reproduction and recruitment (*i.e.* Heitmeyer & Fredrickson 1981; Kaminski & Gluesing 1987). Indeed, body condition is an important factor in waterfowl survival and fitness. For example, Devries *et al.* (2008) found that female Mallard which arrive in better condition on breeding grounds in the Canadian prairie-parklands hatched eggs 15 days earlier than those in relatively poor condition. Guillemain *et al.* (2008) also observed more juveniles during autumn in southern France when body condition of females was greater at the end of the previous winter. Gunnarsson *et al.* (2005) used stable-carbon isotopes to demonstrate that Black-tailed Godwits *Limosa limosa* wintering in high quality sites in Europe were more likely to use higher-quality breeding habitats and have greater reproductive success than birds using poorer-quality habitats (see also Norris & Marra 2007).

These and related metrics are useful for understanding cross-seasonal carry-over effects (Harrison *et al.* 2011; Sedinger & Alisauskas 2014), but difficulty lies in the fact that autumn staging and migration immediately follow the breeding season, and are temporally furthest from the next breeding season. Hence, "back-dating" and identifying resources used by birds following their arrival on the breeding grounds, in relation to previous habitat use, are paramount needs. For example, if body condition of a cohort of Mallard in Nebraska in late March was known and these birds were subsequently sampled on the breeding grounds, linking March condition and breeding success seems reasonable (*i.e.* Devries *et al.* 2008). However, how should we consider body condition in relation to future fitness prospects in a cohort of birds examined months earlier, during autumn–winter?

No doubt, fitness is partly a result of some cumulative use of resources during an animal's annual cycle. The greatest uncertainty seems to be in understanding at what point in the non-breeding phase of the cycle a potential shortfall (or indeed windfall) of resources might influence future fitness prospects. There are likely bottlenecks or thresholds related to resource use during the year which could impose disproportionate impacts on subsequent fitness; these may vary considerably between years and across species, and deserve further investigation.

As an alternative to indexing body condition or some other fitness metric, perhaps coordinated inter-regional aerial transect surveys of waterfowl during autumn–spring migration could be conducted (*sensu* Pearse *et al.* 2008) to determine "hot spots" of waterfowl use, thereby identifying and characterising complexes of wetlands and uplands used by the majority of waterfowl (Pearse *et al.* 2012). Aerial survey data could be incorporated with GIS layers to illustrate habitat features and describe high and low priority habitats for North American waterfowl during winter and migration (*e.g.* Pearse 2007), analogous to the "thunderstorm maps" used by waterfowl breeding ground JV programmes (Loesch *et al.* 2012). Clearly, we must be creative in engaging diverse human expertise and reliable technologies to understand the ecology of waterfowl throughout their annual cycle and range, then use this knowledge to conserve important habitats for birds across the Holarctic region and worldwide.

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**Photograph:** A spring of Green-winged and Blue-winged Teal wintering in Louisiana, by Charlie Hohorst.