Nest site selection by Holarctic waterfowl: a multi-level review

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Abstract

Because of birds' mobility, behaviour and many species' migratory nature, they select repeatedly and spatially among habitats and have been central figures in studies of avian breeding habitat selection during the 20th and 21st centuries. The scientific literature on habitat use by breeding waterfowl has origins dating back to the writings of Charles Darwin in *The Voyage of the Beagle*, wherein he described the distribution and habitat differences of two species of geese on the Falkland Islands. Since that time, waterfowl ecologists have gone from descriptive studies of nest site characteristics used for planning waterfowl conservation and management to comparing nest site use in relation to potential habitat availability and determining selection for a wide array of ecological correlates. Waterfowl ecologists most recently have been investigating the adaptive significance of nest site selection by associating the latter with individual fitness and demographic measurements to assess the birds' adaptability under environmental conditions at multiple scales of selection. While little direct assessment of 1st and 2nd order nest site selection has occurred (*sensu* Johnson 1980), available information is most consistent with the hypothesis that selection at these scales is driven by food availability. At the 3rd and 4th order of selection, data are consistent with hypotheses that both food availability and predator avoidance drive nest site selection, depending on the species and type of nesting aggregation. We also identify understudied areas of nest site selection important for the conservation and management of waterfowl and suggest that the large-scale influence of current anthropogenic and natural effects on the environment indicates that greater emphasis should be directed toward understanding waterfowl nest site selection at the 1st and 2nd orders of selection and how nesting habitat selection interfaces with community ecology of sympatric breeding waterfowl. Moreover, because habitat selection of pre-fledging waterfowl is inherently linked to breeding habitat selection, we suggest an updated review of brood habitat selection should ensue from our synthesis here.

Key words: hierarchal habitat selection, nest, nesting habitat, nest site selection, waterfowl.

Elucidation of use and selection of habitat by animals for breeding and other life-history segments during their annual cycle is essential for answering basic ecological and applied questions at the individual, population and community levels (Fretwell & Lucas 1969; Lack 1971; Cody 1981). Because of birds' mobility and many species' migratory nature, they select repeatedly and spatially among habitats and have been central to studies of breeding habitat selection during the 20th and 21st centuries (Grinnell 1914; Lack 1933; Hildén 1965; Cody 1985; Block & Brennan 1993).

The scientific literature on habitat use by breeding waterfowl has origins dating back to the writings of Charles Darwin in The Voyage of the Beagle wherein he described distribution and habitat differences of the "Upland Goose" *Anas magellanica* and the "Rock Goose" *Anas antarctica*, although it appears he was describing what are now considered subspecies of upland geese *Chloephaga picta leucoptera* and *C. p. picta* on the Falkland Islands. Oberholser & McAtee (1920) reported on population declines in waterfowl in North America, exhorted the benefits of eliminating spring harvest in North America for its resultant increase in waterfowl populations. Displaying considerable insight for their time, they recognised the importance of habitat by suggesting that agricultural land development was negatively affecting duck populations through decreased availability of crucial wetlands and other habitats. Although early conservationists were beginning to recognise the importance of preserving breeding habitat for the conservation of wildlife populations

(Leopold 1933), only sporadic reports of waterfowl nest sites can be found in the scientific literature until a synthesised description of the nesting habitats for waterfowl in North America was published by Bent (1923). Although Bent reviewed the available information, data were lacking on species-specific use of nesting habitats. This lack of understanding was also apparent in Pirnie's (1935) book on waterfowl ecology and management in Michigan. He recommended planting junipers *Juniperus* sp. and pine *Pinus* sp., or other evergreens and other shrubby vegetation, as nesting cover for upland game birds including Mallard *Anas platyrhynchos*, and other ducks nesting in uplands in Michigan. He later noted, however, an abundance of successfully nesting ducks in flooded meadows that provided dense herbaceous cover. Likely in response to the decreasing abundance of waterfowl in North America during the drought stricken 1930s and early 1940s, numerous descriptions of waterfowl nesting habitat were published in the mid 20th century (*e.g.* Bennet 1938; Low 1941; Gross 1945; Leitch 1951). Indeed, recognition became prevalent in the 1950s that factors including habitat type, social avoidance and attraction, and predator avoidance may influence species-specific nest site selection (*e.g.* Earl 1950; Kossack 1950; Glover 1956). As biologists recognised that nesting habitat use varied by species and even within species, and that habitat choices influenced reproductive success, considerable effort was spent during the 1960s–1980s describing species-specific variation in nesting habitat and how such variation was influenced by predation pressure (*e.g.* Keith 1961; Duebbert & Lokemoen 1976; Weller 1979;

Livezey 1981; McLandress 1983; Kaminski & Weller 1992). These studies emphasised the applied aspects of the data in identifying habitat use patterns for conservation and management purposes, but rarely used the data specifically to advance understanding of causative drivers of waterfowl habitat selection (*cf.* Kaminski & Prince 1984; Cody 1985) despite the fact that the early habitat selection models were developed and widely tested at that time (Fretwell & Lucas 1969; Fretwell 1972). Furthermore, because dabbling and diving ducks tend to breed in temperate, lower latitude regions than arctic nesting swans, geese and sea ducks, their habitat has undergone increased anthropogenic modifications. However, even the more northern boreal regions that were once relatively immune to human developments are now influenced by both direct (forest harvest, mining, extraction of fossil fuels and wind power development) and indirect (atmospheric warming, airborne pollution and eutrophication) anthropogenic forces. Indeed, the rate of anthropogenic modification has recently increased dramatically in some boreal regions in the northern hemisphere (Murphy & Romanuk 2014).

In general, factors that influence waterfowl reproduction are thought to have the greatest influence on populations of generally *r*-selected species (dabbling and diving ducks; Flint *et al.* 1998; Hoekman *et al.* 2002; Coluccy *et al.* 2008), while factors that influence post-fledging survival tend to have a greater influence on population dynamics of more *K*-selected species (sea ducks, geese, and swans; Nichols *et al.* 1976; Cooch *et al.* 2001; Schamber *et al.* 2009). Managers

have recognised these distinctions and accordingly often tend to focus their effort toward managing habitat that influences reproductive success for dabbling and diving ducks while managing non-breeding habitat and harvest for sea ducks, geese and swans.

Thus, because reproductive success has strong influence on population dynamics, understanding breeding habitat use and selection is fundamental for wise decisions regarding habitat conservation and management. This recognition has led to numerous detailed studies of how management actions influence habitat selection and nest success of boreal and temperate nesting dabbling and diving ducks. Additionally, possibly because of influential writings by Romseburg (1981) and Walters (1985), waterfowl biologists have begun to view breeding habitat selection in basic and applied ecological contexts (*e.g.* Nudds 1983; Clark & Shutler 1999; Fast *et al.* 2007). This change coincided with recognition that spatial scale is an important factor in the habitat selection process (Johnson 1980; Hutto 1985; Wiens 1989). Thus, issues of spatial and temporal scale have been influential in framing and articulating theories on which research about breeding habitat selection in waterfowl is based (Johnson 1980; Hutto 1985; Forbes & Kaiser 1994). Selection of habitat by waterfowl during breeding and other annual cycle events may be viewed as a hierarchal process. For example, selection of nest sites is a fine-grained hierarchical process with individuals utilising large-grain characteristics for initial (first order) selections of geographic regions, then using

characteristics that can be distinguished at more reduced grain size as the selection process continues (Johnson 1980; Wiens 1989; Kristan 2006). Grain size for nesting waterfowl generally will be smaller than other habitat components of the annual cycle, except perhaps individual foraging and rest sites, because nests occupy microhabitats and their location is such an important aspect of reproductive success (O'Neila *et al.* 1986; Wiens 1989).

In this contribution, we review the characteristics waterfowl use to make decisions at various spatial levels leading downward to nest site selection, the selective pressures that affect those characteristics, and the resulting fitness of those decisions. We review how research on waterfowl nest site selection has influenced our understanding of basic ecological theory and how this information is used when making management decisions. To facilitate comparison of cross taxa variation, this paper is partitioned into four scales of selection: 1st order – general region or latitude, 2nd order – landscape type (biome) within a region, 3rd order – location, wetland, or upland within a landscape and 4th order – specific nest site within the location (Kaminski & Elmberg 2014). By organising the review in this manner, we hope to articulate benefits of life-history comparisons. We conclude by identifying areas where information is inadequate to answer basic ecological questions and make reliable conservation decisions.

First-order selection

Habitat selection at this scale is best addressed by considering studies asking questions associated with diversity, distribution, and abundance of organisms at the continental scale. Brown & Maurer (1989) coined the term "macrocecolgical approach" to describe ecological approaches of this scale. They stated, "Our goal is to understand the assembly of continental biotas in terms of how the physical space and nutritional resources of large areas are divided among diverse species." Two areas of study that often use a macroecological approach to address associations among space and resource availability and species distribution, abundance and diversity are migration and community ecology; thus, these should provide insight into 1st order nest site selection of waterfowl are migration and community ecology (*e.g.* Davis *et al.* 2014).

Most waterfowl species occurring in the Holarctic are long- to medium-distance migrants. A general pattern among these waterfowl is they nest in temperate, sub-arctic and arctic regions too inhospitable to support them during the non-breeding period, and then spend the non-breeding period in locations with more moderate climates (Bellrose 1980; Kaminski & Weller 1992). Thus, if we assume pursuit of nesting habitat begins when birds begin to transition from non-breeding to breeding periods, the initial consideration for 1st order selection is really a question of migration (*i.e.* Does an individual breed at the same location it spent the non-breeding period or move to a different location?). Considerable debate exists whether migration evolved from northern and temperate breeding populations migrating south during the non-breeding season as winter ensued or from

sub- and tropical breeding locations as species expanded their range into more seasonal, higher latitudes after Pleistocene glaciation (Cox 1968; Chesser & Levey 1998; Alerstam *et al.* 2003). Regardless of origin and mechanistic stimuli of migration, the Cordillerin and Laurentide ice sheets in North America and the Scandinavian ice sheet in Europe during the most recent glaciation (from *c.* 120,000–8,500 years ago) generally limited the distribution of waterfowl to regions that serve primarily as wintering areas under current climatic conditions (*e.g.* Hawkins & Porter 2003; Hortal *et al.* 2011). Thus, most species of Holarctic waterfowl since glaciation have evolved strategies to migrate north to breed. A number of hypotheses have been proposed to explain northern latitude breeding, including migration as a method to exploit rich seasonal food resources, avoid predation, reduce exposure to disease and parasites, exploit latitudes with long day lengths during the growing season, or reduce intra- or interspecific competition (Cox 1985; Fretwell 1980; Alerstam & Högstedt 1982; Piersma 1997; Chesser & Levey 1998; Rappole & Jones 2002).

The tendency for Holarctic waterfowl to migrate from southern wintering regions to more northern breeding regions has created a somewhat unique pattern of species richness. While species richness of most organisms, including most bird taxa, decreases with increasing latitude, species richness of Holarctic waterfowl tends to peak between 40°–65° latitude, declining rapidly north and south of that range (Dalby *et al.* 2014). Within this range of latitudes, waterfowl inhabit all the major biomes including grassland, temperate rain forest, tundra, taiga, eastern deciduous forest and desert when adequate water is present (Bellrose 1980; NAWMP 2012). The northern range limit for species is most likely driven by the length of the ice-free period being too limited to provide adequate time for reproduction (Schmidt *et al.* 2011), while the factors that influence the southern range limits are generally undefined for Holarctic waterfowl.

As the unique association between species richness and latitude in Holarctic waterfowl demonstrates, 1st order selection for Holarctic waterfowl seems a question of migratory behaviour, because it can influence species distribution which can drive spatial variation in species richness. Thus, an additional ecological concept to gain insight into the selective forces of 1st order selection and the potential driving force behind the southern range limit in Holarctic waterfowl is the concept of community ecology. Nudds (1992) thoroughly reviewed theories on species richness in waterfowl communities. In general, the discussion has changed little since that review. Species richness is dependent on three processes: speciation, extinction and dispersal. The speciation and extinction process influence variation in richness among clades over evolutionary time and potentially large scale (continental) spatial variation, while the dispersal process likely has the greatest influence in ecological time and on more local (regions and less) variation for mobile organisms such as waterfowl (Hulbert & Stegen 2014). Because of the close association between species distribution, migration and species richness,

some of the same selective forces posited to influence migratory behaviour (*i.e.* disease, predation pressure, resource availability and intra- and interspecific competition) as well as other factors such as the species-area relationship, habitat heterogeneity and time for or rate of diversification have been proposed as primary mechanisms for spatial variation in species richness (Arrhenius 1921; Willson 1976; Wright 1983; Evans *et al.* 2005). While none of these mechanisms have been excluded, the roles of time, habitat heterogeneity and resource availability have been accepted as the most likely mechanisms.

A commonly proposed mechanism to explain the decline in species richness with increasing latitude observed in most groups of organisms other than waterfowl is that the former have had a longer period of time to diversify, diversify at a faster rate and have greater niche conservatism in the tropics (*i.e.* long-term stability of the environment conserving the niche); thus, the tropics support greater species richness (Brown 2014). Using similar logic, more recent large scale climatic factors such as glaciation have also been proposed to explain patterns of species richness at the continental scale within the Holarctic (Hawkins & Porter 2003; Hortal *et al.* 2011). If time were the primary mechanism driving the observed relationship between Holarctic waterfowl species richness and latitude, we would predict greater species richness in the more southern latitudes, given that vast areas of the more northern latitudes were glaciated as recently as 8,000 years ago. This prediction is opposite of the present pattern, indicating time is an unlikely explanation.

Total habitat area and heterogeneity also have been found to be a strong predictor and causative agent of species richness for some taxa (Roth 1976; Elmberg *et al.* 1993). If total wetland area or wetland heterogeneity were driving latitudinal variation in waterfowl species distribution, we would predict greater wetland area and heterogeneity in more northern latitudes. We were unable to locate latitudinal data reflecting wetland heterogeneity, but the wetland trends data provide an estimate of total wetland acreage for each of the United States (Dahl 2011). If wetland area is driving the latitudinal variation in waterfowl species richness, we predict an increase in wetland area with latitude. When we regressed total wetland acreage for each state in the United States against its geographic midpoint, we found no relationship between latitude and total wetland acreage for all states ($r^2 = 0.18$, $P = 0.24$) or those states between 80–105° longitude where most nesting waterfowl occur ($r^2 = 0.15$, $P = 0.29$). Furthermore, if we assume the relationship between wetland heterogeneity and wetland area at regional scales is similar to the relationship at more local scales (Elmberg *et al.* 1993, 1994), there should be a strong correlation between total wetland abundance and wetland diversity. Thus, if wetland heterogeneity is driving the relationship between species richness and latitude, we should again detect a positive relationship between latitude and overall wetland acreage, a relationship that contradicts our observation.

The final explanation of latitudinal patterns in waterfowl species richness is resource availability. Resource availability has been found to be strongly correlated to

species richness at multiple scales for a variety of taxa. Latitudinal variation in per capita resource availability could be due to reduced intra- or inter-specific competition in more northern latitudes (Ashmole 1963), more wetlands (or other requisite habitat) in more northern latitudes, or higher productivity in more northern latitudes.

Ashmole (1963) argued that because the inhospitable winter climate of more seasonable environments limited the number of birds breeding in temperate regions, there was greater per capita resource availability. This argument does not appear to hold true for waterfowl, however, in that both abundance and richness peak at higher latitudes.

In recent large scale studies, resource availability seems to be the best predictor of species richness for the majority of taxa (Hawkins *et al.* 2003; Hulbert & Haskell 2003; Evans *et al.* 2005). As the analysis described above indicates, relative surface area of wetlands, assuming a correlation between surface area and heterogeneity, wetland heterogeneity does not appear to increase with latitude in North America but our analyses currently are restricted to this continent. Thus, if resource availability is the driving mechanism for latitudinal variation in waterfowl species richness, a latitudinal trend in per area resource availability may be the driving mechanism. Resource availability per area may vary due to greater exploitation by waterfowl in more southern wetlands or greater per area productivity in higher latitude wetlands.

During winter, waterfowl congregate in regions that provide predictable food availability (*i.e.* remain unfrozen) exploiting leafy vegetation, seeds, tubers and agricultural seeds produced during the previous growing season, as well as aquatic invertebrates. The high concentration of waterfowl exploiting these resources likely reduces their availability to waterfowl as winter progresses and transitions to spring (Davis *et al.* 2014). Thus, it's possible the exploitation of resources by wintering waterfowl reduces the resources to migrating and breeding waterfowl, reducing the species richness and abundance in more southern latitudes.

Alternatively, a similar amount of wetlands in more northern latitudes could provide more resources if vegetation in more northern regions provides greater benefit to secondary consumers (Coley *et al.* 1985; Moles *et al.* 2011; Morrison & Hay 2012). Vegetation with greater nutritional value would directly influence resource availability for geese which are herbivorous throughout their annual cycle and produce young that require nutrient rich plants during early post-hatch growth (Coley *et al.* 1985; Sedinger 1992). Nutritional quality of vegetation could also influence ducks that are primarily carnivorous during the breeding season by providing substrates and food for aquatic invertebrates that ducks consume (Krapu & Reinecke 1992). Because most vegetation in higher latitude wetlands continues to grow until freezing temperatures cause senescence, annual rate of plant decomposition is much lower in more northern wetlands (Webster & Benfield 1986; Magee 1993; Holt 2008). Thus, as opposed to more southern wetlands where plant decomposition and nutrient turnover continues throughout the winter with little remaining by spring, there

is considerable organic material and a large food base for invertebrates when spring arrives at more northern latitudes. Moreover, seeds and invertebrates are not exposed to predation by birds during the winter, providing returning breeders with a less depleted food base than is the case in more southern latitudes where wetlands are used year round by resident and seasonally occurring species of waterbirds. Additionally, a number of studies have demonstrated that invertebrates prefer to forage on plant material in more northern latitudes (*e.g.* Pennings *et al.* 2001, 2007). Some have suggested this strategy is due to fewer chemical defences from plants from more northern latitudes while others have suggested it is due to higher concentrations of nitrogen (Coley *et al.* 1985; Moles *et al.* 2011; Morrison & Hay 2012). Regardless of the mechanism, vegetation from more northern latitudes appears to be of greater nutritional value to invertebrates and herbivorous waterfowl, potentially producing greater nutritional resources.

Finally, as Willson (1976) suggested the shorter growing season in more northern latitudes may itself lead to an increase in standing biomass of aquatic invertebrates. The briefer period for reproduction may cause more species of invertebrates to reproduce simultaneously, leading to a higher spike in overall invertebrate biomass in more seasonal northern environments. High-latitude wetlands may thus offer a high standing biomass and higher per capita food resource availability when waterfowl nest as a result of higher productivity, concurrent food peaks or a long period without food depletion (Danell & Sjöberg 1977).

Although other mechanisms for explaining the more northern latitudinal peak in species richness of waterfowl cannot be excluded, per capita nutrient availability appears to have the greatest level of support (Dalby *et al.* 2014). While at a more regional scale, waterfowl richness appears to increase with both nutrient availability and habitat heterogeneity (2nd order level selection; Elmberg *et al.* 1993). Although the nutrient availability hypothesis appears to be most consistent with data currently available, direct tests with empirical data have not been conducted. For example, no one has tested for general latitudinal variation in aquatic invertebrate biomass (*cf.* Arzel *et al.* 2009 for a one-species all-flyway example), and although evidence exists indicating vegetation from more northern areas may be preferred by invertebrates over the same species of vegetation from more southern latitudes, studies have not isolated confounding effects of chemical or physical defence and concentration of nutrients for the more northern vegetation.

Second-order selection

Often waterfowl have multiple options for choice of biome (*e.g.* grassland, forest, tundra) to select for nest sites even after selecting a geographic latitude in which to breed. Unlike latitudinal variation in species richness, there appears no clear pattern in species richness across various northern hemispheric biomes. In fact, although some species appear to be habitat specialists in that most individuals are found almost exclusively in one biome (*e.g.* Blue-winged Teal *Anas discors* in grassland and Green-winged Teal/Eurasian Teal *A. crecca* in

boreal environs), most species appear to be habitat generalists, selecting specific nest site characteristics regardless of the biome and thus can be found in multiple biomes (*e.g.* Nicolai *et al.* 2005; Safine & Lindberg 2007). Furthermore, with the exception of cavity nesting species, which largely require forested habitat, or sea ducks that specialise in coastal waters for brood rearing, almost all species can be found nesting in multiple biomes. Even species like the Common Eider *Somateria mollissima*, which depend on marine environments for foraging and are considered a tundra nesting species in North America, will nest in island forests when such forests are in close proximity to brood habitat (Öst *et al.* 2008a).

Species that demonstrate a clear preference also have likely adapted to specialise on certain characteristics of habitat (Mulhern *et al.* 1985). The two selection factors that appear to be acting most at the scales of 3rd and 4th order selection are food availability and predator avoidance, making them good candidates for proximate cues that may drive 2nd order selection. While nest predation pressure potentially varies with latitude (Hanski *et al.* 1991; Elmberg *et al.* 2009), it doesn't appear to vary among biomes so selection of biome may be dictated by food availability (Grand & Flint 1997; Fournier & Hines 2001; Walker *et al.* 2005; Schamber *et al.* 2009; *cf.* Elmberg *et al.* 2009). Currently, increasing exploitation of natural resources of the tundra and boreal regions emphasises the need to better understand the requirements of habitat specialists for future management and conservation. Studies addressing the question of whether the limited breeding

ranges overlap between Blue- and Green-winged Teal or Gadwall *A. strepera* and American Wigeon *A. americana*, species that breed in different biomes but appear closely related genetically and ecologically, is due to variation in habitat requirements or competition may help elucidate questions associated with 2nd order selection.

Third-order selection

Third-order selection is the level at which they select a specific local habitat(s) within a biome. A number of nest site selection characteristics discussed here also could be considered 4th order characteristics. We consider them 3rd order characteristics for the sake of this discussion due to the grain size at which the characteristic may have been measured. For example, if a characteristic was measured at a scale that was relevant to more than one female (*i.e.* a field or patch of trees), we considered it 3rd order selection; whereas, if a characteristic was measured at a scale relevant to one female (*e.g.* density of vegetation surrounding a specific prospective nest or size in the opening of a tree cavity), we considered it 4th order selection. In the following sections, we review potential ecological, environmental or social influences of 3rd order selection of nest habitats.

Predator and coexisting prey densities

Nest predation is the primary cause of nest failure in waterfowl (Sargeant & Raveling 1992; Stephens *et al.* 2005). Egg predators are distributed heterogeneously across landscapes concentrating in habitats that provide efficient foraging (Kuehl & Clark 2002; Phillips *et al.* 2003; Elmberg & Gunnarsson 2007; Klug *et al.* 2009) and

protection from higher trophic level predators (Crabtree *et al.* 1989; Dion *et al.* 2000; Chalfoun *et al.* 2002). High nest predation and heterogeneous distribution of predators invoke selective pressure for waterfowl to adapt strategies of selecting nest habitats and sites with fewer predators or more coexisting prey than other potential sites, leading to a reduction in nest predation (Holt 1977; Ackerman 2002; Eichholz *et al.* 2012).

Predator avoidance appears to be the primary selective force for colonial nesting species, apparently having less impact on dispersed nesting species (Schmutz *et al.* 1983; Bousfield & Syroechkovskiy 1985; Fox *et al.* 2009). This inconsistency may be related to the level of feeding that occurs by females during incubation and the distance young can travel after hatch. Most colonial nesting species of waterfowl, with the possible exception of Black Brant *Branta bernicla nigricans* and Ross's Goose *Chen rossii*, feed little, if any, during incubation and often travel long distances from nests to brood rearing locations; thus, there appears to be little pressure to nest near high concentrations of food for females and goslings. Although Black Brant often travel a substantial distance from nest sites to brood rearing areas, females spend as much as of 20% of the incubation period off the nest in maintenance activities such as feeding (Eichholz & Sedinger 1999; Sedinger *et al.* 2004). Brant colonies typically are located near the coast where nutritious foods are available and Arctic Fox *Vulpes lagopus* numbers are reduced due to fall flooding from storm surges (Mickelson 1975; Raveling 1989).

Researchers have long assumed nest site selection was influenced by predator avoidance, but only recently has there been evidence that birds could assess local predator density and modify their behaviour accordingly. Fontaine & Martin (2006) found numerous species of passerines modify their reproductive investment by increasing their feeding behaviour when predator abundance was reduced, but provided no explanation as to the mechanism parents used to assess predator density. Similarly, Dassow *et al.* (2012) found evidence that ground nesting ducks modify reproductive investment based on density of predators (*cf.* Duebbert & Kantrud 1974). A number of studies have now provided evidence that birds are able to use various mechanisms to assess predator abundance and modify reproductive strategies (*e.g.* Lima 2009; Eichholz *et al.* 2012; Forsman *et al.* 2012). Additionally, researchers conducting predator exclusion and reduction studies have observed increases in nesting densities in areas where predators were reduced. Although greater adult philopatry and an increase in the abundance of breeding yearlings associated with increased nest success and natal philopatry are typically proposed as the mechanisms for this increase (Duebbert & Kantrud 1974; Duebbert & Lokemoen 1980; Garrettson & Rohwer 2001), these results also are consistent with the idea that waterfowl select sites with reduced predator abundance, thus immigrating into experimental areas. Although results from studies consistent with the idea that waterfowl have developed a mechanism for assessing predator abundance and avoiding areas of high predator density, further

empirical evidence is needed to test this hypothesis.

In addition to predator density, coexisting prey density may play a role in nest site selection. A number of studies have found a correlation between coexisting prey abundance and nest success in tundra, taiga and temperate grasslands (Pehrsson 1986; Summers *et al.* 1994; Ackerman 2002; Brook *et al.* 2008; Iles *et al.* 2013). For some tundra nesting species, the relationship between nest success and coexisting prey appears adequate to cause certain populations of waterfowl to modify nesting distribution or forgo nesting in years when prey abundance is low (Underhill *et al.* 1993; Sittler *et al.* 2000; Quakenbush *et al.* 2004). Researchers cannot explain whether decreased reproductive investment is due to a lack of coexisting prey (Bêty *et al.* 2001, 2002; Gauthier 2004; Iles *et al.* 2013) or "protective umbrella" species – species of predatory birds that inadvertently defend other birds' nest from mammalian predators while defending their own nest (Dyrcz *et al.* 1981). The mechanism(s) by which waterfowl assess abundance of coexisting prey is also unclear. A potential mechanism may be use of mammalian urine similar to that demonstrated for raptors. Evidence consistent with the hypothesis that predatory birds use UV light reflecting off phosphorous in mammal urine to locate areas of high prey density is well documented (*e.g.* Viitala *et al.* 1995; Koivula & Viitala 1999; Probst *et al.* 2002). Ducks can also see into the UV light spectrum (Jane & Bowmaker 1988) and may use a technique similar to that described by Eichholz *et al.* (2012) to assess indirectly coexisting prey abundance. This hypothesis, however, has

not been tested empirically. Furthermore, while a pattern of increased nesting effort and success in years of greater small mammal abundance is well established in arctic and subarctic regions, the relationship is less clear in temperate regions, potentially due to greater abundance of generalist predators (Hanski *et al.* 1991). Perhaps an increase in abundance of coexisting prey, such as other waterfowl or bird eggs, arthropods or small mammals, would produce a functional response by satiating or decreasing movement of predators, thus decreasing susceptibility of nests to predation (Crabtree & Wolfe 1988; Crabtree *et al.* 1989; Larivière & Messier 2001; Ackerman 2002). In contrast, increased abundance of coexisting prey may produce a numerical response by concentrating predators into areas of high abundance of coexisting prey, decreasing waterfowl nest success (Holt & Lawton 1994). In the only known experimental study of nesting ducks belonging to different guilds (*i.e.* tree cavity *versus* ground nesters), Elmberg & Pöysä (2011) found that adding ground nests near cavity nests did not increase predation risk for the latter in an area where the main nest predator (Pine Marten *Martes martes*) was a genuine generalist. Clearly, the interrelationships between waterfowl nest success, predator abundance and coexisting prey abundance are complex and unresolved. A lack of consistent results between nest success and coexisting prey may be due to the variability in the balance between the strength of functional and numerical responses associated with varying species of predators and abundance of coexisting prey (Ackerman 2002; Brook *et al.* 2008), making predictions uncertain about how coexisting prey

distribution should impact nest site selection by waterfowl.

Food availability

Non-breeding or abandonment of reproductive attempts have been observed in Northern Pintail *Anas acuta* (Derksen & Eldridge 1980), Mallard (Krapu *et al.* 1983) and Lesser Snow Geese *Chen caerulescens* (Ankney & MacInnes 1978), indicating that securing adequate resources is an important component of reproductive success. Thus, in contrast to colonial nesting species, a number of studies have found that dispersed nesting waterfowl nest in areas where food for adults during incubation and post-hatch young is available (Swanson *et al.* 1974; Derksen & Eldridge 1980; Haszard & Clark 2007; Fox *et al.* 2009). This phenomenon may be because dispersed nesting waterfowl tend to be smaller bodied than colonial nesting species, thus are required to feed more during incubation, or tend to nest amid more structurally complex vegetation that limits overland movement of young. For example, a number of studies have found reduced survival associated with increased overland movement of dispersed nesting females and broods (Rotella & Ratti 1992; Pearse & Ratti 2004; Simpson *et al.* 2005; Krapu *et al.* 2006; Davis *et al.* 2007); however, other studies have found no relationship (Talent *et al.* 1983; Dzus & Clark 1997; Pöysä & Paasivaara 2006). In contrast, colonial nesting species, such as Snow and Barnacle Geese have adapted to travel long distances from nest sites to brood sites to maximise fitness, indicating little cost to overland travel (Larsson & Forslund 1991; Sedinger 1992; Aubin *et al.* 1993; Cooch *et al.* 1993).

Interspecific Associations

Multiple studies have found evidence that subarctic and arctic nesting species nest in association with large avian predators even though the same predators prey on young waterfowl (Young & Titman 1986; Underhill *et al.* 1993; Summers *et al.* 1994; Quakenbush *et al.* 2004; van Kleef *et al.* 2007). In the process of deterring mammalian predators from their own nests, these avian predators inadvertently deter mammalian predators from nearby waterfowl nests. Thus, waterfowl selecting nests within a protective umbrella of predatory birds may gain benefits of egg protection that outweigh potential predation of hatchlings (Vermeer 1968; Young & Titman 1986; Bird & Donehower 2008). Some have suggested the extent of this protection is so important for some species that certain individuals will forgo breeding in years when predatory birds are not present to provide protection (Underhill *et al.* 1993; Summers *et al.* 1994; Quakenbush *et al.* 2000). In addition to nesting in association with predatory species, smaller waterfowl may enjoy fitness benefits by nesting near large waterfowl that deter small and medium-sized predators (McLandress 1983; Baldwin *et al.* 2011). For example, Canada Geese are known to reduce predation on and increase species richness of co-nesting ducks (Fabricius & Norgren 1987; Allard & Gilchrist 2002). To date, such relationships between predatory birds, colonial birds and dispersed nesting waterfowl have been reported mainly from arctic biota, but Fabricius & Norgren (1997) observed diving and dabbling ducks nesting close to geese on islets in archipelagos in the

temperate biome. We see no reason why this should not be a widespread phenomenon, suggesting it should be investigated more thoroughly.

Nesting congregations

Lack (1965) suggested that birds have evolved two primary forms of nest distribution, colonial and dispersed nesting. In waterfowl, however, there appears to be a gradient from dense to loose colonies for some species to species generally considered dispersed nesters, but congregate into nest "clumps" or nest in high densities on islands. Here, we partition the discussion of nesting congregations into three sections: (1) coloniality – which pertains to species that generally congregate when nesting, (2) clump nesting – pertaining congregations of typically dispersed nesters in contiguous upland habitat, and (3) island congregations – typically dispersed nesters are found nesting in congregations on islands.

Coloniality

Coloniality appears to be the evolved trait from the ancestral condition of dispersed nesting (Coulson & Dixon 1979; Wittenberger & Hunt 1985; Rolland et al. 1998) and may have evolved multiple times due to a variety of selective pressures (Siegel-Causey & Kharitonov 1990; Rolland et al. 1998). One reason this topic has garnered substantial attention is the few measured benefits (advantages linked to predation and enhanced food finding) relative to costs of colonial nesting (competition for food, nest sites and mates, increased conspicuousness, transfer of disease and parasites, cannibalism; Siegel-Causey & Kharitonov

1990; Rolland et al. 1998). The most recent discussions of the evolution of colonial nesting suggest it evolves through: (1) a "limitation of breeding site" framework where a lack of nesting sites force individuals to nest in aggregation with no net benefit (Wittenberger & Hunt 1985), (2) an "economic" framework where a cost-benefit tradeoff of specific habitat conditions favour coloniality (Alexander 1974; Wittenberger & Hunt 1985; Sachs et al. 2007), or (3) a "by-product" framework where individual habitat selections or sexual selection leads to aggregation and colonial breeding results from these individual selection decisions not as a direct result of being aggregated (Wagner et al. 2000; Wagner & Danchin 2003; Sachs et al. 2007).

To our knowledge, no studies have been conducted directly to address theories on the evolution of coloniality in waterfowl; however, a number of studies appear to be consistent with factors described under the "economic" framework. For Holarctic waterfowl, evolution of coloniality has been limited to species that generally breed in open tundra, although admittedly it is a matter of definition whether intra- and interspecific aggregation of nests on islands in prairies and archipelagos in temperate and boreal regions should be construed as colonial nesting. Because open tundra makes nest concealment difficult, this observation appears consistent with the hypothesis that open habitat favours coloniality over dispersed nests as a means of predator avoidance. Indeed, positive correlations between colony size and density and nest success appear consistent with this hypothesis (Bousfield & Syroechkovskiy

1985; Raveling 1989). Furthermore, the species of waterfowl that commonly nest colonially generally feed little during incubation; thus, shared information of feeding sites appears unlikely to exert considerable selective pressure for coloniality (Milne 1976; Korshgen 1977; Parker & Holms 1990; Erikstad & Tveraa 1995).

Food availability during brood rearing, however, may be influential for evolution of coloniality in waterfowl. A number of studies have now documented reduced growth rate of goslings with increased colony size, observations consistent with a cost associated with colonial nesting (Cooch *et al.* 1991; Larsson & Forslund 1991; Sedinger *et al.* 1998). In the case of Black Brant, however, grazing pressure from high densities of colonial geese appeared to maintain quality grazing lawns; thus, colonial behaviour appears to impact nutrient availability positively for young brant (Person *et al.* 2003; Nicolai *et al.* 2008). Hence, with currently available data, factors associated with the "economic" framework seem most likely to explain the evolution of coloniality in waterfowl; however, the specific mechanism(s) is still unclear and may vary among species.

Clump nesting

With exception of a few species of sea ducks and geese, waterfowl are generally dispersed nesters (Anderson & Titman 1992). An unusual phenomenon often described by researchers, but yet to be explained, is the clumping of nests in relatively uniform habitat (Duebbert & Lokemoen 1976; Hines & Mitchell 1983; Fowler *et al.* 2004; Fowler 2005). In theory, this behaviour contradicts the strategy of dispersed nesting, because nests become concentrated, allowing for possible functional or numerical responses by predators (Tinbergen *et al.* 1967; Holt 1977). Studies have found evidence for negative density dependence, no density dependence, and positive density dependence of nests in both artificial and natural nest studies (Duebbert & Lokemoen 1976; Andrén 1991; Major & Kendal 1996; Larivière & Messier 1998; Sovada *et al.* 2000; Ackerman *et al.* 2004; Gunnarsson & Elmberg 2008). Inconsistency in results among studies likely is due to variation in the numerical (Holt 1977) and functional response behaviour of predatory species (Holling 1965; Tinbergen *et al.* 1967), variations in the response behaviour of prey, in the scale of the studies and in the habitat condition in which predators and prey exist (Grand & Flint 1997; Flint *et al.* 2006; Ringelman *et al.* 2012). Thus, the adaptive costs and benefits of nesting within close proximity of heterospecifics and conspecifics are not well understood.

Clump nesting may be adaptive and due to multiple individuals selecting nest sites in locations with fewer predators (Eichholz *et al.* 2012; Forsman *et al.* 2012), selection by multiple individuals of a yet unidentified nest site characteristic that provides appropriate nest microclimate or safe habitat such as sites that more adequately disperse scent of nests and hens (Conover 2007), rate of homing by successful hens (Greenwood 1982; Hepp & Kennamer 1992; Blums *et al.* 2003; Öst *et al.* 2011), natal philopatry of young (Hines & Mitchell 1983; Lindberg & Sedinger 1997; Coulton *et al.* 2011), or social attraction and transfer of information (Hines &

Mitchell 1983; Pöysä 2006; Valone 2007). Alternatively, in the case of negative density dependence and survival, clumped nesting may even be maladaptive behaviour, being due to environmental change outpacing the ability of birds to adapt, creating a false signal for appropriate nest site selection (Dessborn *et al.* 2011). Because clumping behaviour may appear obtuse evolutionarily and with regard to conservation ramifications, a better understanding of the mechanistic characteristics of this behaviour and its adaptive significance is needed.

Natural islands and island congregations

A number of species prefer islands as nest sites (Ryder 1972; Gosser & Conover 1999; Traylor *et al.* 2004; Öst *et al.* 2011). Island nesting is thought to be beneficial because important nest predators such as skunks, badgers and foxes generally avoid water (Ryder 1972; Mickelson 1975; Thompson & Raveling 1987; Petersen 1990; Zoellick *et al.* 2004). An interesting aspect of island nesting is that a number of species of ducks and geese tend to nest at densities as much as two orders of magnitude greater than densities observed on the mainland (Hammond & Mann 1956; Dwernychuk & Boag 1972; Duebbert *et al.* 1983; Willms & Crawford 1989). This occurrence is especially surprising for species such as Canada geese that typically are extremely territorial, maintaining territories as large as ≥ 100 m around the nest on mainland. The mechanism(s) allowing extremely high nesting density in territorial species may be due to decreased predation pressure leading to fewer individuals attempting to maintain

widely dispersed nests or the inability of early nesters to defend territories and maintain dispersed nests because of an overwhelming drive of individuals to nest on islands (Mack *et al.* 2003). The latter explanation appears most likely based on the extreme number of pursuit flights emanating from islands during early nesting (Duebbert 1966). An additional likely prerequisite for dense nesting congregations on island is adequate food resources to support high densities of adults and young.

Wetland proximity

Primary and secondary productivity during summer dry seasons in the Holarctic is often concentrated around wetlands (Greenwood *et al.* 1995; Larivière & Messier 2000). Greater primary productivity within and immediately adjacent to local complexes of wetlands is thought to increase secondary productivity, concentrating higher trophic organisms, including predators, near wetlands (Greenwood *et al.* 1995; Larivière & Messier 2000). In theory, birds should nest away from wetlands, where predators are less abundant (Robb & Bookhout 1995; Pasitchniak-Arts *et al.* 1998a; Phillips *et al.* 2003; Traylor *et al.* 2004; *cf.* Keith 1961). For wetland dependent precocial species, such as waterfowl, shorter travel distance from the nest to brooding habitats may induce selective pressure to nest close to wetlands (Duncan 1987). Furthermore, most ducks make daily or multiple feeding bouts per day, leading to an additional energetic constraint for nesting far from wetlands (Shutler *et al.* 1998). Thus, most waterfowl species face a trade-off between nesting farther from wetlands, where hatching success may be

increased, with nesting closer to wetlands where duckling survival is maximised (Dzubin & Gollop 1972; Ball *et al.* 1975; Duncan 1987; Pöysä *et al.* 1999). The nest site distance from wetlands that maximises fitness likely varies among species with different life history traits (Duncan 1987). This prediction is supported by various studies finding Northern Shoveler *Anas clypeata* and Blue-winged Teal nesting closer to water than other species or random sites while Northern Pintails nest farther from water than other duck species (Dzubin & Gollop 1972; Ball *et al.* 1975; Livezey 1981; Shutler *et al.* 1998). Studies comparing nesting distance from water between mainland and islands also have found results consistent with this tradeoff. Individuals nesting on islands secluded from mammalian predators selected nest sites nearer to water, suggesting the threat of predation associated with different landscapes and nest substrates may affect the distance that females build nests to water (Kellet & Alisauskas 1997; Bentzen *et al.* 2009).

Habitat fragmentation

Historically, pristine nesting landscapes for waterfowl, whether in temperate forests, grasslands, or sub-arctic boreal and tundra, were vast mosaics of upland and wetlands. However, agriculture, forestry, damming for hydroelectric power and other human development have fragmented these landscapes, especially temperate uplands, making habitat patch size a potentially recent evolutionary nest site selection characteristic (Clark & Nudds 1991; Reynolds *et al.* 2001).

To become a selected trait, patch size would need to influence fitness predictably

for an adequate period of time (Clark & Shutler 1999). Because of benefits associated with widely distributed nests, a generally accepted paradigm is large patches of habitat are better for production and fitness of birds than small patches (Ball *et al.* 1995; Greenwood *et al.* 1995; Reynolds *et al.* 2001). Smaller patches are thought to be less productive because they increase foraging efficiency of predators by providing proportionally more edge habitat, increase density of foraging predators (*i.e.* concentration of enemies hypothesis), force birds to nest in greater density, impact species composition of predator communities, provide more homogeneous vegetation facilitating movement of predators, or increase dispersal inhibiting maintenance of higher concentrations and more intact communities (Higgins 1977; Clark & Nudds 1991; Stephens *et al.* 2004; Bayard & Elphic 2010).

Selection of larger patches should lead to a positive relationship between nest density and patch size, termed area sensitivity (Robbins *et al.* 1989; Bender *et al.* 1998; Conner *et al.* 2000). When considering breeding density and patch size relationships for a wide diversity of fauna, a neutral relationship due to equilibrium theory of biogeography tends to be most supported (Bender *et al.* 1998; Conner *et al.* 2000). For avifauna, area sensitivity due to resource concentration (more resources in larger patches) or concentration of enemies (higher concentration of predators in smaller patches) often garners greatest support (Raupp & Denno 1979; Conner *et al.* 2000). For example, Ribic *et al.* (2009) reviewed statistically rigorous studies of 32 species of

obligate grassland passerines and noted evidence for area sensitivity in half of those species. The review by Ribic *et al.* (2009), and work of other researchers, suggested that area sensitivity is strongest for forest dwelling species relative to grassland species (Conner *et al.* 2000; Bayard & Elphick 2010), and proposed that area sensitivity appears to ignore the potential negative impacts of negative density dependence on nest success discussed earlier.

For upland nesting ducks breeding in the Prairie Pothole Region in North America, where habitat fragmentation has been most dramatic, available evidence is inconsistent with the area sensitivity hypothesis (Clark & Nudds 1991; Arnold *et al.* 2007; Haffele 2012). There are a number of reasons why one may not expect to observe a nest density-patch size relationship for upland nesting ducks when considering mechanisms typically invoked to explain area sensitivity in passerines. In forested landscapes and tall grass prairies adjacent to forests, edges typically result in an intermediate scrub-shrub habitat that decreases nest success by concentrating predators; thus, birds should select nest sites farther from habitat edges (Johnston & Odum 1956; Root 1973; Gates & Gysel 1978; Vickery *et al.* 1992). Because larger more uniform patches would allow birds to select nest sites farther from edge, larger patches are thought to be beneficial (Gates & Gysel 1978; Pasitchniak-Arts & Messier 1996; Clark & Shutler 1999). Although edge effects on nest success appear intuitive and have been well documented in some landscapes (Root 1973; Gates & Gysel 1978; Whitcomb *et al.* 1981; Sliwinski & Koper 2012), empirical evidence

supporting the relationship among birds nesting in mixed and short grass prairies, where most temperate upland nesting waterfowl nest, remains inconsistent (Sargeant *et al.* 1984; Krasowski & Nudds 1986; Clark & Nudds 1991; Horn *et al.* 2005). In short and mixed grass prairie grasslands, patch edges tend to be very distinct, with no transitional zones, and perhaps these abrupt edges don't attract predators (Pasitchniak-Arts & Messier 1998; Phillips *et al.* 2003; Horn *et al.* 2005). Additionally, grasslands tend to support both core and edge predators, making predation more distributed across the landscape (Bergin *et al.* 2000; Chalfoun *et al.* 2002; Winter *et al.* 2006).

An alternative mechanism for area sensitivity in grassland birds is the "concentration of enemies" hypothesis (Conner *et al.* 2000). This mechanism hypothesises that predators respond numerically or behaviourally to fragmentation in the landscape, leading to a positive relationship between patch size and fitness of birds. Smaller patches may allow a predator to modify its behaviour by concentrating foraging effort in remaining grassland, increasing the likelihood a predator encounters a nest regardless of nest density. Additionally, smaller patches may be more attractive to predators, thus increasing their abundance and concentration within the patch (Root 1973; Sovada *et al.* 2000; Kuehl & Clark 2002). Although this theory appears intuitive, empirical support for the hypothesis is conflicting, with results of studies being both consistent (Fritzell 1975; Oetting & Dixon 1975; Cowardin *et al.* 1985; Johnson & Shaffer 1987) and inconsistent with this hypothesis (Duebbert & Lokemoen

1976; Livezey 1981; Vickery *et al.* 1992; Esler & Grand 1993; Phillips *et al.* 2004).

The remaining alternative explanations of area sensitivity in grassland birds are associated with greater resource availability in larger patches. Resource availability is often found to influence habitat selection and breeding distribution of wildlife (Stephens & Krebs 1986). Studies often find evidence for area sensitivity with no corollary relationship in productivity, suggesting that resource availability is the probable mechanism (Van Horn 1983; Bock & Jones 2004; Winter *et al.* 2006). While this explanation is intuitive for passerines, which acquire most resources from upland landscapes, most resources for ducks are gleaned from wetlands during breeding seasons, whereas grassland and other uplands merely provide cover for nests. In fact, for grassland nesting species of waterfowl, which may not be as susceptible to edge effects and acquire resources from wetlands, inverse area sensitivity often is predicted between nesting density and patch size (MacArthur *et al.* 1972; Pasitchniak-Arts *et al.* 1998; Sovada *et al.* 2000; Donovan & Lamberson 2001). Similar to the mechanism proposed for predators in the concentration of enemies hypothesis, habitat fragmentation hypothetically forces birds to nest densely in remnant cover, potentially leading to "ecological traps" (Clark & Nudds 1991; Ball *et al.* 1995; Reynolds *et al.* 2001). This hypothesis assumes bird population abundance is at some level independent of grassland abundance, so when grasslands are reduced, birds modify distributions but do not exhibit an isometric decline in abundance, leading to inverse area sensitivity (Braun *et al.* 1978; Clark & Nudds 1991;

Greenwood *et al.* 1995). Such an outcome may be especially relevant to upland nesting waterfowl in grasslands and many authors have suggested this mechanism has led to a decline in reproductive success of these birds (Greenwood *et al.* 1995; Sovada *et al.* 2000; Reynolds *et al.* 2001). Assuming wetland resources drive waterfowl distribution, even if waterfowl have adapted to select large patches, fragmentation and loss of grasslands have potentially forced them to nest in remnant patches near wetlands that may not be the preferred patch size, obscuring any relationship between patch size and nest density.

Finally, habitat fragmentation may not have been enacting selective pressures on ducks for an adequate period of time to evolve an adaptation. The majority of the fragmentation of prairie grassland has occurred since the 1950s and fragmentation of boreal forest is even more recent. Although selective pressures that directly influence species demographics tend to evolve quickly, 60 generations may not be adequate time for a behavioural adaptation such as the selection of large patches to occur especially considering that breeding individuals may not be reproductively successful annually during their longevity.

In summary, unlike forest birds, evidence for area sensitivity or a positive relationship between reproductive success and patch size for grassland birds in short or mixed grass prairies is equivocal. Furthermore, the few studies that have tested for a breeding density:patch size relationship were not consistent with the prediction of area sensitivity or inverse area sensitivity typically proposed in studies associated with habitat

fragmentation. The limited number of studies that address this question appears surprising considering patch size plays such an important role in habitat conservation and restoration.

Fourth-order selection

This level of selection has been the focus of most waterfowl nesting studies (Kaminski & Weller 1992). While predator avoidance and food availability for adults and young likely play a strong role in 1st–3rd orders of nest site selection, predator avoidance seems the predominant selective force for 4th order selection. Nest site selection likely influences predation rate and most female annual mortality occurs during the breeding season (Ricklefs 1969; Southwood 1977; Hoekman *et al.* 2002).

Nest-site characteristics are well documented for many species of birds including waterfowl and are often found to be significantly different from characteristics at randomly selected locations (Bellrose 1980; Clark & Shutler 1999). This non-random distribution is usually assumed to be caused by habitat preference and thus adaptive (Martin 1998; Clark & Shutler 1999). Preferred nest site characteristics have been described in numerous studies, but evidence of their adaptive value is inconsistent and limited (Hines & Mitchell 1983; Crabtree *et al.* 1989; Clark & Shutler 1999; Durham & Afton 2003). This inconsistency is at least partially due to species-specific variation; geographic, temporal and design variation of studies; focus on restricted components of the ecological community (*i.e.* only waterfowl and predators, waterfowl and vegetation, or predators and vegetation); and short

study durations (2–3 years) preventing inference regarding short- versus long-term variation (Clark & Nudds 1991). Additionally, dramatic anthropogenic changes to natural environments since the 20th century may have caused some nest sites selection characteristics to become maladaptive traits as environmental change outpaced adaptive ability of birds (Dwernychuk & Boag 1972; van Riper 1984; Schlaepfer *et al.* 2002). Herein, we review characteristics proposed as 4th order nest site characteristics of waterfowl and their level of empirical support.

Vegetation structure

Evidence supports the notion that physical structure of the vegetation is an important criterion of nest site selection for almost all species of ground and over-water nesting waterfowl (McLandress 1983; Miller *et al.* 2007; Safine & Lindberg 2008; Haffele *et al.* 2013). Two characteristics that have been identified as important, especially for many ground-nesting ducks, are height and density of vegetation. In general, they appear to select taller and thicker vegetation (Schrank 1972; Martin 1993; Clark & Shutler 1999; Haffele *et al.* 2013). Cover height appears to be most important when the primary predators are avian but also can be important when mammalian predators such as Striped Skunks *Mephitis mephitis* are the primary predator (Hines & Mitchell 1983; Crabtree *et al.* 1989), whereas cover density is most important when the primary predators are mammalian (Schrank 1972; Bowman & Harris 1980; Livezey 1981; Hines & Mitchell 1983; Rangen *et al.* 2000). Height and density of cover may directly impact success by

obstructing movement of predators, increasing abundance of alternative prey, providing visual obstruction, or obstructing distribution of scent. While a large number of studies have found waterfowl select specific structural characteristics of vegetation for nesting, studies testing for the adaptive benefit have been inconsistent with only a few studies finding a positive relationship with nest success (Glover 1956; Crabtree *et al*. 1989; Clark & Shutler 1999; Durham & Afton 2003). The inconsistency of results among studies likely is due to variation in methodology and scale, the complex relationship between life history characteristics, cover characteristics, types of predators, availability of alternative prey or a combination of these other factors (Clark & Nudds 1991; Horn *et al*. 2005; Haffele 2012).

Some authors have proposed a tradeoff between concealment of the eggs from predation (current reproductive investment) and escaping from predation (future reproductive investment) leading to selection of cover of an intermediate height and density (Götmark *et al*.1995; Traylor *et al*. 2004; Miller *et al*. 2007; McRoberts *et al*. 2012); however, evidence supporting the selection of cover height or density as a stabilising selective trait is equivocal (Keith 1961; Duncan 1986; Clark & Shutler 1999; Haffele *et al*. 2013). Additionally, for some species, likely because cover > 45 cm tends to shade out shorter vegetation and thereby reduces density at ground level, nest success appears to be greatest when cover is at an intermediate height (16–45 cm; Crabtree *et al*. 1989; Haffele *et al*. 2013); thus, the perceived tradeoff between current and future reproductive success is not necessary

for selection of intermediate nest cover height to occur in ground nesting birds (Hines & Mitchell 1983; Crabtree *et al*. 1989; Durham & Afton 2003; Haffele *et al*. 2013).

Level of reproductive investment varies among species based on the likelihood of future productivity (Fontaine & Martin 2006; Dassow *et al*. 2012). Theoretically, factors that influence 4th order nest site selection, such as vegetation height, should vary among bird species based on life-history traits leading to interspecific variation (Grant & Shaffer 2012). This theoretical relationship is supported among closely related species of ducks; shorter lived species that invest more into current reproduction tend to nest in more dense cover (Keith 1961; Duncan 1986; Greenwood *et al*. 1995; Haffele 2012). This interspecific variation in nesting cover requirements should be recognised when planning and implementing conservation and restoration of waterfowl nesting habitats and not establish only uniform dense nesting covers (Keith 1961; Livezey 1981; Lokemoen *et al*. 1990; Greenwood *et al*. 1995).

Specific composition of cover

Species composition of vegetation can influence nest site selection and success, and preferred vegetative composition varies among closely related species (Keith 1961; Duncan 1986; Crabtree *et al*. 1989; Lokemoen *et al*. 1990). Crabtree *et al*. (1989) found nest success to be greatest in vegetation composed of grasses and forbs and surmised this combination provided greater concealment by grasses at lower levels and forbs at higher levels. Although physical characteristics of vegetative cover likely have the greatest influence on nest site selection by

birds (Schrank 1972; Gilbert *et al.* 1996), factors influenced by vegetative species composition itself also may directly or indirectly influence nest site selection. For example, although measures of height and density did not discern differences between forbs and grasses, Blue winged Teal and Northern Shoveler tended to select sites with more grasses while Mallard and Gadwall selected sites with more forbs (Livezey 1981; Lokemoen *et al.* 1990; Clark & Shutler 1999). These researchers could not discern if these differences in selection were due to smaller bodied teal being constrained by robust forbs, a difference in unmeasured characteristics such as overhead cover, or a direct selection for preferred species of vegetation. For example, certain species of vegetation being preferred or avoided as nest sites due to their ability to disrupt scent plumes of birds and nests (Aylor *et al.* 1993; Conover 2007). Regardless of the cause, because of the continuous loss of nesting cover in temperate regions of North America and replacement of native vegetation with exotic species, understanding the degree of specificity or level of plasticity in this trait may be important for determining the necessary composition of nesting cover that maximises benefits to waterfowl. Choosing a specific plant species to provide cover is a process that also has a component of phenology and between-year variation in the advancement of spring. This is especially true for early nesting species such as Mallard and Northern Pintail, which often start nest-building and egg-laying before the present year's plants provide cover adequate for nesting. Accordingly, in early nesting species, evergreens and last year's vegetation may act as cues for hens

prospecting for nest sites. An issue related to this is the potential mismatch between nesting timetable of waterfowl and vegetation development that may arise as a consequence of global climate change (Drever & Clark 2007). If these processes become uncoupled, decreased nest success may result, which may ultimately affect population trajectories (Drever *et al.* 2012).

Vegetative litter and remnant down

Aldo Leopold (1933) first proposed leaf litter was an important component of nest site selection and success for ground nesting birds. The overall importance of litter depth in selection of nest-sites has been documented for certain grassland songbirds (Winter 1999; Davis 2005; Fisher & Davis 2010), but the relative importance for waterfowl is largely unknown. Leaf litter and remnant down may be important for providing the appropriate thermal microenvironment and concealing eggs from predation, especially for early nesting species prior to emergence of new vegetation (Bue *et al.* 1952; Duebbert 1969; Fast *et al.* 2010; Haffele 2012). Alternatively, depth of remnant leaf litter may be used as a predictor for the amount of vegetation that can be expected to grow in that location later in the nesting season (Haffele 2012). Height and amount of leaf litter were important factors for nest site selection by early (Mallard, Northern Pintail), intermediate (Blue-winged Teal) and late nesting ducks (Gadwall and Northern Shoveler; Haffele 2012). Haffele (2012) found strong selection by ducks for nest sites with deeper leaf litter, and found nest sites with more litter had lower nest mortality. Furthermore, Common

Eiders initiated nesting earlier in nest bowls with experimentally increased amount of down suggesting preference for nest bowls with remnant down from the previous year's nesting attempt. However, during heavy snow years, both Cackling Geese *Branta hutchinsii* and Emperor Geese *Chen canagica* selected sites with more short dead vegetation (Petersen 1990; Fast *et al.* 2010).

Microclimate

In addition to shielding the nest and hen from predators, nest site selection influences physical conditions of incubation such as shelter from wind, relative humidity, precipitation and excessive solar radiation diurnally and loss nocturnally (Walsberg 1981). Because the vast majority of egg mortality comes from predation with only a minor component of embryonic mortality associated with nest microclimate, studies associating nest site selection with microclimate are few relative to those associating nest site selection with predation. For example, Gloutney & Clark (1997) investigated the influence of nest site selection of Mallard and Blue-winged Teal on nest microclimate and concluded selective pressure of optimising physical conditions of incubation is secondary to the selective pressures of egg and hen survival, based on a combined measure of temperature and relative humidity. More recently, however, evidence is accumulating indicating the impact of the nest microclimate is not limited to the immediate impact of embryonic mortality but can influence both short- and long-term fitness of the adults and young, thus benefits associated with favourable microclimates

may not be immediately recognised (Wilson & Verbeek 1995; Zicus *et al.* 2004; Hepp *et al.* 2006; Fast *et al.* 2007; DuRant *et al.* 2011). Furthermore, the cost of incubating eggs with less than optimal microclimates can affect the adult's ability to care for young and adult survive post hatch (Erikstad & Tveraa 1995; Öst *et al.* 2003). Selecting nest sites that minimise energetic costs of incubation could be especially important for smaller bodied species nesting in temperate areas or larger bodied species in arctic and sub-arctic regions (Piersma *et al.* 2003; Hilton *et al.* 2004). Selecting nest sites that provide appropriate insulation could come at a cost to nest concealment, leading to a tradeoff between appropriate microclimate and concealment (Shutler *et al.* 1998). Finally, nest site micro-climate could indirectly influence risk of predation by influencing incubation behaviour of adults. Less insulated clutches could be more energetically expensive to incubate forcing hens to leave the nest more to feed, thus increasing susceptibility to egg predation (Thompson & Raveling 1987; Afton & Paulus 1992; Durrant *et al.* 2011). Because of the limited amount of interest this area has received and the potential demographic impact of reduced reproduction, more studies simultaneously considering the impact of nest site selection on microclimate, predator avoidance and the long-term ramifications on fitness of both adults and young seem warranted.

Date of ice or snow melt

To breed successfully, the ice- and snow-free period must be sufficient for waterfowl to lay and incubate eggs, for young to grow and for young and moulting adults to attain flight and

acquire adequate nutrient reserves to sustain them for the first stage of the fall migration. Because the amount of time to achieve these stages of the annual cycle is so limited, there is strong selective pressure for females to initiate nesting as soon as possible at latitudes where the time window for successful breeding may be limiting. Earlier nest initiation for arctic and subarctic breeding species has been found to influence nest survival, growth rates of young, adult body size, year of first breeding and first year survival; which are vital rates that influence individual fitness (Lindholm *et al.* 1994; Sedinger *et al.* 1995; Cooch 2002; Blums *et al.* 2005; Pilotte *et al.* 2014). This strong selective pressure for early nest initiation has caused the date that potential nesting sites become snow free to be an important component of nest site selection in species breeding in arctic habitats (Ely & Raveling 1984; Petersen 1990; Chaulk *et al.* 2007; Lecomte *et al.* 2008). Because winter winds often sweep snow from the highest potential nest sites, the date a nest site becomes ice or snow free is often strongly correlated to the height of the nest site. Thus, when selecting the first snow-free sites, waterfowl are often selecting for sites with higher elevation in the area (Mickelson 1975; Eisenhauer & Kirkpatrick 1977; Peterson 1990). Selection of higher nesting sites also has been reported in more temperate areas, likely decreasing the potential for flooding and increasing probability for early snow melt from tallest sites (Jarvis & Harris 1967; Ely & Raveling 1984; O'Neil 1988).

Kinship

For some semi- and colonial nesting species or for clumps of nests of dispersed nesting species, related individuals have been found to nest in closer proximity than would be expected under a random distribution (van der Jeugd *et al.* 2002; Fowler *et al.* 2004; Sonsthagen *et al.* 2010). Clusters of related individuals can arise due to adult and natal breeding philopatry, phenotype matching, and kinship associations (Ely & Scribner 1994; van der Jeugd *et al.* 2002; Fowler *et al.* 2004; Sonsthagen *et al.* 2010). However, evidence is consistent with the idea that individuals actively seek nest sites near closely related individuals (van der Jeugd *et al.* 2002; Sonsthagen *et al.* 2010; Fishman *et al.* 2011). For example, Barnacle Geese have been observed nesting near their siblings from the same brood on islands different from their natal island, indicating nesting proximity was not due to natal philopatry (van der Jeugd *et al.* 2002). A similar observation was not made regarding sisters from different broods (*i.e.* different years), a result most consistent with the hypothesis females are actively selecting nest sites near known kin (van der Jeugd *et al.* 2002). At this point, benefits of selecting nest sites near kin are speculative but may include increased willingness for cooperation in predator defence, joint defence of high quality food patches and relatives with which they share heredity, or decreased aggression between related neighbours (van der Jeugd *et al.* 2002; Sonsthagen *et al.* 2010; Fishman *et al.* 2011).

Fidelity, experience and information sharing

The costs and benefits of nest site fidelity and complementary behaviour of dispersal are thought to be an influential component of

nest site selection (Hinde 1956; Greenwood 1982). There are a number of proposed advantages to exhibiting fidelity to a nesting site, including familiarity with food and other resources and with neighbours decreasing aggressive interactions (Greenwood 1982), all of which may ramify into to greater productivity (Harvey *et al.* 1979; Newton & Marquiss 1982; Gratto *et al.* 1985; Korpimäki 1988). One particularly important factor influencing an individual's decision to maintain breeding site fidelity or disperse appears to be past reproductive success. Making nest site selection decisions based on past experiences would require some level of consistency in the success of specific nest site. Although there often appears to be substantial annual variability in nest success within a nesting location (Haffele *et al.* 2013; Ringelman 2014), other studies have documented consistency in security of nest sites, such as nest cavities used by Common Goldeneyes *Bucephala clangula* (Elmberg & Pöysä 2011). Therefore, a number of studies have found migratory birds disperse farther when they fail in a reproductive attempt (Weatherhead & Boak 1986; Paton & Edwards 1996). This behaviour also has been observed in waterfowl, with a positive relationship between degree of fidelity and fecundity (MacInnes & Dunn 1988; Hepp & Kennamer 1992; Lindberg & Sedinger 1997; Öst *et al.* 2011).

In addition to the individual's past reproductive success, a number of studies have provided evidence that birds use success of neighbours (public information) to make initial nest site selection or determine whether to disperse or exhibit spatial fidelity (Boulinier *et al.* 1996; Doligez

et al. 2003; Valone 2007). For waterfowl, there is some evidence of hetero- and conspecific attraction (Elmberg *et al.* 1997; Pöysä *et al.* 1998); however, use of public information for nest sites selection is only speculative for ground nesting birds and has received limited support for cavity nesting species (Pöysä 2006; Ringelman *et al.* 2012; *cf.* Roy *et al.* 2009).

Obstacles and structures

In addition to vegetation, waterfowl nesting in open landscapes, such as tundra, often use obstacles such as rocks or drift wood to conceal nests from predators and increase quality of the nesting microclimate (Ryder 1972; Noel *et al.* 2005; Fast *et al.* 2007; Öst & Steele 2010). Waterfowl nesting in association with such obstacles have been reported to have higher nest success and reduced weight loss during incubation (Kilpi & Lindström 1997; Öst *et al.* 2008b; Öst & Steele 2010). Similar to waterfowl nesting in vegetation, however, there appears to be a tradeoff between level of concealment and the ability of incubating hens to detect and quickly escape from predators (Öst *et al.* 2008a; Öst & Steele 2010).

Nesting cavities

A somewhat unique adaptation evolved by a number of birds including waterfowl is nesting in tree and artificial cavities. Birds likely began nesting in cavities in an effort to avoid nest predation (Lack 1954; Nilsson 1986). Ducks are secondary cavity nesters that rely on tree holes excavated by other wildlife, natural formation through injury to trees and subsequent decay, or nest boxes erected by humans (Bellrose & Holms 1994;

Nielsen *et al.* 2007). Although cavities were once thought to be limited in North America for Wood Duck *Aix sponsa*; this may no longer be the pervasive reality in most areas (Soulliere 1988; Nielsen *et al.* 2007; Denton *et al.* 2012). Lowney & Hill (1989), however, reported that densities of cavities suitable for Wood Duck nesting (*i.e.* adequate dimensions and internal surface for eggs) in Mississippi hardwood bottomlands were among the lowest reported for mature forests in North America. Additionally, in more northern regions of Europe and North America, areas where cavities are used by Smew *Mergellus albellus* and *Bucephala* species, cavities are still thought to limit some populations (Savard 1988; Pöysä & Pöysä 2002; Vaillancourt *et al.* 2009; Robert *et al.* 2010), mainly because natural forests contain many more old and hollow trees than do modern managed forests. Thus, some suggest nest box programmes are important to maintain breeding populations of cavity nesting ducks in some regions (Lowney & Hill 1989).

Although over-water cavities would intuitively appear to be more secure and nest success has been found to be higher during periods of flood (Nielsen & Gates 2007), there appears to be no clear selection for over-water cavities for Wood Ducks. However, Wood Duck duckling survival was greatest for individuals hatched in predator-protected nest structures located amidst flooded scrub-shrub wetlands in Mississippi, which may have concealed nest structures from avian egg predators during egg laying and incubation or provided near cover for hens and broods after exodus from the nest (Davis *et al.* 2007, 2009). Moreover, regarding natural cavities, cavity characteristics appear to be more important than the cavity tree characteristics when ducks are selecting nest sites (Robb & Brookhout 1995; Yetter *et al.* 1999). Cavities used by waterfowl have been found to be higher from the ground or water, nearer forest opening or wetlands, and have entrances with smaller widths and heights (Prince 1968; Dow & Fredga 1985; Yetter *et al.* 1999; Robert *et al.* 2010). All of these characteristics have been found to reduce the potential for predation. Orientation of cavity entrance could also be important for nest microclimate (Gilmer *et al.* 1978), and while distance to wetlands was important for Common Goldeneyes (Pöysä *et al.* 1999), it did not appear to have a strong influence on cavity use by Wood Ducks (Robb & Bookhout 1995).

Conclusions and implications

Throughout the 20th and 21st centuries, both environmental impacts and conservation-management actions to remediate those impacts for breeding waterfowl have occurred on characteristics that affect nest site selection at the local or patch and microhabitat scales (*i.e.* 3rd and 4th order selection), those likely based almost entirely on more fine-grained interactions (Hutto 1985; Kaspari *et al.* 2010). The outcomes of habitat selection decisions at 3rd and 4th order scales influence species compositions of waterfowl communities in breeding areas, which may influence predator-prey relationships and competition for resources on an ecological time scale and behavioural and morphological characteristics on an evolutionary scale (Morris 2003). Outcomes from these intrinsic interactions likely provided selective

forces acting upon individuals which may have influenced their 1st and 2nd order selection. Additionally, whether hierarchical habitat selection by migratory waterfowl is driven by bottom-up, top-down, or both processes in different time and space scales on individual survival and reproductive success remains intriguing and worthy of research (Kaminski & Elmberg 2014). Moreover, 1st order scales of selection of migratory waterfowl operate at a continental context and generally determine distribution or range limits of species, while 2nd order scales of selection often determine habitat(s) used within a biome(s) in which species and individuals distribute themselves. Decisions at the 1st and 2nd level seem based on large-grain abiotic (*e.g.* wetland system characteristics, climate, and landscape configurations) and biotic characteristics (*e.g.* terrestrial and aquatic communities) that may be perceived from a long distance but likely have developed through novel or philopatric experiences at smaller scales (Hutto 1985). Hutto (1985) termed these large-grained characteristics "extrinsic characteristics" because they are external to local habitats or patches; thus, these characteristics may not lend themselves to manipulation by management and conservation actions. Observed patterns from 1st and 2nd order selection are results of processes in evolutionary (ultimate factors) more than in ecological time frames (proximate factors) and are likely maintained through adult and natal philopatry (Klomp 1953; Hutto 1985). Even in migrants, like most waterfowl, glaciation and concurrent biome and climate shifts are background long-term influences of species pools and hence of

present regional community composition. Nevertheless, the ecological time frame lets us study range expansions and retractions and abundance shifts relative to abiotic and biotic conditions. Both are important agents shaping waterfowl and other wildlife distributions and communities in the past and present (*e.g.* Schummer *et al.* 2010; Pearse *et al.* 2010). Furthermore, the scale has changed at which ecologists now recognise anthropogenic activities are modifying the environment. Climate change and the additive effects of natural resource exploitation and agricultural development by humans are now recognised to influence the environment at the scale of the biome or continent; thus, understanding ecological questions at a larger scale through macroecological studies will become more relevant for the management and conservation of waterfowl. As this review indicates, however, studies of 1st and 2nd order waterfowl nest site selection are relatively few and often indirect, forcing us to speculate based on results of 3rd and 4th order selection. Thus, an increased emphasis on studies addressing 1st and 2nd orders of habitat selection appears warranted. Yet, we must recognise that some characteristics are changing at the granular level of 1st and 2nd order selection and may be manifested or detected in 3rd or 4th orders of selection studies through outcomes of individual distribution, survival and reproductive success. Thus, even studies addressing 1st and 2nd order selection should associate the outcome of those selection decisions at the level of the individuals to understand processes and patterns promoting fitness.

We also recognise the process of nest site

selection interacts strongly with the process of community ecological development, yet most studies of this process are limited to very few components of the community (*e.g.* vegetation characteristics and nest success or predator abundance and nest success) and often only one or two small and often ambiguously defined landscape scales. We suggest the simplistic approach that has dominated past studies has limited our ability to understand the process of nest selection, limiting management and conservation actions; thus, a multi-scale community approach of study is warranted. This approach might best be achieved by following the advice of Bloom *et al.* (2013) and incorporating both habitat selection and demographic variables in the modelling process. We also recognise questions of causality are best addressed

Table 1. Non-ranked priority recommendations for future research on nest site (habitat) selection in waterfowl, derived but adapted from 16 suggestions proposed by Kaminski and Weller (1992). We recognise that a number of the recommendations address recruitment, whereas this review was limited to nest site selection. Thus, our recommendations are limited to the nest site selection component of recruitment.

Priority	Recommendation
1	Relate habitat selection to waterfowl survival and recruitment rate.
2	Test models and determine the effects on recruitment of possible inter and intra-specific density-dependent habitat selection.
3	Determine effects of different densities and communities of predators and prey on waterfowl habitat selection and how that process interacts with scale and community of vegetation.
4	Invoke hierarchical approaches in studies of habitat selection by individuals to obtain data on individuals' habitat use throughout their annual cycle and range for incorporation into population models and to guide habitat conservation planning and implementation.
5	Relate long-term changes in wetland and upland composition to corresponding changes in the variety of interacting factors (*e.g.* vegetation, food, predators and competitors) that influence waterfowl recruitment at multiple scales.
6	Determine effects of variation and loss in availability of intermittently, temporarily, and seasonally flooded wetlands on waterfowl habitat selection, dispersal and recruitment.
7	Determine the effect of habitat fragmentation on waterfowl habitat selection and community organisation.

through manipulative experiments; however, experimental studies are inherently difficult and costly to carry out at larger scales. This dilemma is a true challenge for waterfowl and wildlife research, conservation and management, but it deserves resolution and implementation through landscape-scale cooperatives of ecological and conservation partners.

Kaminski & Weller (1992) produced a thorough review of breeding habitats of Nearctic waterfowl. At the conclusion of their review, they identified 16 issues which they believed needed further study. Here, we suggest that a slightly modified list of seven of those 16 issues warrant priority consideration (Table 1). We conclude that only the first of the 16 recommendations has been explored with sufficient replication using species of adequately diverse life histories to allow for general inference and management actions, although some unique species of conservation concern are exceptions. This observation corroborates our assertion that the advancement in understanding the process of nest site selection has been limited by approach.

Finally, the time required to complete the task of reviewing thoroughly the substantial literature on multi-scale nest site selection by Holarctic waterfowl has prevented us from addressing habitat selection by broods, a second but no less important component of breeding habitat selection. In fact, a recent Mallard study suggests potential tradeoffs between nest site and brood habitat selection, suggesting simultaneous integration of these may be most appropriate for future studies (Bloom *et al*. 2013). We recommend undertaking the task of updating and advancing reviews of waterfowl pre-fledging ecology and summarising the current status of information regarding 3rd and 4th order brood site selection (*e.g.* Sedinger 1992), given that 1st and 2nd order selection occur at the time of nest site selection and were covered in this review.

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