An introduction to habitat use and selection by waterfowl in the northern hemisphere

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Abstract

This introductory article aims to provide a theoretical framework to the topics of habitat use and selection by waterfowl (*i.e.* family Anatidae) in the northern hemisphere during the four stages of their annual cycle: autumn migration and winter, spring migration and pre-breeding, nesting and brood rearing, and post-breeding and moulting. Papers addressing each of these seasonal sectors of the annual cycle, which follow this introduction, were presented at the 6th North American Duck Symposium, "Ecology and Conservation of North American Waterfowl" in Memphis, Tennessee in January 2013. Here, we consider the theory and selected empirical evidence relevant to waterfowl habitat and resource use and selection that may affect individual survival and fitness of waterfowl in Nearctic and Palearctic ecozones. Additionally, where possible, a comparative taxonomic approach is attempted in the following papers to identify and generalise patterns in habitat and resource use and selection across waterfowl taxa that may influence biological outcomes for individuals, populations and species through space and time. Each of the subsequent papers use accumulated science-based information to recommend future opportunities and strategies for research and for habitat and population conservation. Collectively, our goals in synthesising information on waterfowl are to help sustain harvestable populations of waterfowl and to protect rare species amid worldwide changes in climate, landscape, economics, socio-politics and growth of human populations.

Key words: Anatidae, annual cycle, biological outcome, conservation, fitness, habitat, habitat use, habitat and resource selection, management, survival, waterfowl.

Habitat is a principal unifying entity and concept in wildlife ecology and conservation, because wildlife would not exist in the absence of habitat and associated resources (Block & Brennan 1993). The English word "habitat" is derived from the Latin word "*habito*," meaning "to live or inhabit." Herein, we define habitat as environmental space occupied by living individuals of a species for any amount of time during their life cycle and which contains resources for individual survival and reproduction (Block & Brennan 1993; Jones 2001). All waterfowl species (*i.e.* ducks, geese and swans: Anatidae) of the northern hemisphere use three-dimensional habitat space (*i.e.* aerial, terrestrial and aquatic habitats) and the resources therein for physiological maintenance during their annual cycle and ultimately to gain fitness (*i.e.* individual survival and reproductive success resulting in genetic representation in subsequent generations; Mayr 1970). Generally, use of only two-dimensional space (terrestrial and aquatic) by waterfowl has been quantified using modern analyses and technologies (Belant *et al.* 2012; *cf.* O'Neal *et al.* 2010). Nonetheless, much literature exists which provides evidence that habitats and associated resources impose critical influences on individuals and evolution of adaptive strategies (Hildén 1965; Lack 1968; Stearns 1976, 1992; Southwood 1977, 1988; Kaminski & Weller 1992; Block & Brennan 1993; Jones 2001).

Block and Brennan (1993) and Jones (2001) provided excellent reviews of habitat use and selection and related concepts, primarily based on the ornithological literature. To resolve and reduce future ambiguity in terminology, they clarified and defined terms such as habitat, niche, habitat selection (or preference) and habitat suitability, and we have adopted their terminology here for consistency. The simplest and most common measure of habitat use by individuals of a species is their occurrence within habitats. Habitat associations (or correlations) are demonstrated quantitatively when animals' presence or abundance varies with measured habitat features (Wiens 1976, 1985). However, habitat associations should not be construed as habitat or resource selection, because selection is influenced by availability including accessibility and procurement (hereafter, availability) of habitats and associated resources (Block & Brennan 1993; Garshelis 2000; Jones 2001). Although unlikely to happen in nature, Fretwell and Lucas (1970), Fretwell (1972) and Wiens (1976, 1977, 1985) hypothesised that "true" habitat selection occurs when animals use habitats disproportionately to their availability and resource quality without constraints from extrinsic factors such as predation, competition, territoriality, density dependence, anthropogenic effects or a combination of these and other factors. Likely, habitat selection has evolved through increased immediate or short-term benefits to individuals using specific habitats and resources, leading to long-term rewards in survival, reproduction, and fitness accrued through natural selection and possibly other agents of evolution (*e.g.* gene flow; Lack 1968; Wilson & Bossert 1971; Jones 2001). Demonstration of causal linkages between cross-seasonal and habitat-resource use and fitness is difficult, especially for migratory waterfowl because of disconnects in daily to seasonal use of resources to meet physiological and behavioural needs during the annual cycle. Therefore, researchers generally infer habitat and resource selection when these are used disproportionately in relation to their estimated availability (Johnson 1980; Mulhern *et al.* 1985; Alldredge & Ratti 1986; Jones 2001). For example, Mulhern *et al.* (1985) proposed and tested three theoretical models of habitat use by Mallard *Anas platyrhynhos* and Blue-winged Teal *Anas discors* in relation to habitat availability, based on structural characteristics of used and available wetlands: 1) no selection when use of habitats "mapped" availability, 2) "plastic" selection when use was statistically different from available wetlands but use was temporally dynamic, and 3) "stenotopic" (*i.e.* specialistic or static) selection when use was statistically different from available wetlands but was consistent through time despite varying availability. Therefore, here and in subsequent papers in this section on seasonal habitat use, the term "habitat selection" is used when referring to results of studies that have demonstrated disproportionate habitat or resource use, or relationships between one or both of these and measures of biological outcomes (*i.e.* metrics of individual condition or performance (fitness correlates); Chalfoun & Martin 2007; Ayers *et al.* 2013).

Habitat use and selection by migratory birds, such as most waterfowl, may be envisioned as a multi-stage, hierarchical process from macro- to micro-spatial scales throughout the birds' annual cycle and geographic range (Johnson 1980). However, spatial distributions of waterfowl and other gregarious animals may not be completely influenced by individuals or habitat and resources. For example, habitat use by male waterfowl is often influenced by female philopatry to natal or other areas in their annual range, and juvenile birds, without prior migratory or dispersal experience, are likely influenced by co-occurring conspecifics or closely related taxa with similar niches (Brennan & Block 1993; Elmberg *et al.* 1997; Thomson *et al.* 2003). Despite possible social effects on habitat and resource use, migratory waterfowl seemingly make an initial "first-order" selection of geographic regions, such as those important to the birds during breeding and non-breeding seasons (Johnson 1980; Baldassarre & Bolen 2006). Within first-order occupied regions, waterfowl make "second-order" selections of wetland systems (Cowardin *et al.* 1979) and possibly associated landscapes (*e.g.* nesting habitats or arable fields for foraging). Next, they make "third-order" selections of local, site-specific wetlands or other locations and finally "fourth-order" selections of microhabitats where individuals specifically may roost, nest, forage or engage in other activities to acquire food or other resources including mates (Wiens 1973; Johnson 1980; Kaminski & Weller 1992, Baldassarre & Bolen 2006). Considering non-migratory species that do not move seasonally among geographic regions (*e.g.* subtropical species; Mottled Duck *Anas fulvigula*), their local-regional, annual home range and inclusive habitats constitute their "first-order" selected habitats, followed hierarchically by second- to fourth-orders of selected habitats within their home range as described above for migratory species (*sensu* Jones 2001). Additionally, the reversal of this process from micro- to macro-habitats also can be envisioned when birds depart microhabitats to disperse or migrate to different areas and habitats therein.

Ideally, habitat use and selection should be investigated at all relevant spatio-temporal scales to identify the scale(s) at which possible limiting factors may have greatest impacts on survival, reproduction and fitness. The outcome of habitat use and selection analyses can be influenced by the spatio-temporal scale of the investigation and associated environmental variation (Wiens 1985). Moreover, habitat use and selection should be studied among individuals of different ages, sexes and social status to yield accurate inferences and effectively guide conservation at population and species levels, always recognising that some habitat use by individuals may be related to presence and abundance of related or unrelated species (*e.g.* Götmark 1989; Jones 2001). Additionally, Buskirk and Millspaugh (2006) stated that an informative metric of habitat use may be risk to fitness (*e.g.* the probability of individual mortality; Lima & Dill 1990). Nonetheless, Ayers *et al.* (2013) and Lancaster (2013) recommended that researchers should measure individually based biological outcomes resulting from habitat and resource use, because the population-level approach common in wildlife-resource studies limits ability to make inferences about the importance of habitats and resources by failing to link these with fitness metrics or masking effects through sampling error or model averaging. Indeed, population-level habitat use and selection processes merely reflect the sum of individual responses; thus, individual-based approaches should be emphasised because natural selection operates at this level and individuals vary (*e.g.* Block & Brennan 1993; Goss-Custard *et al.* 1995; Stillman 2008).

Given that habitat quality or suitability (*sensu* Fretwell & Lucas 1970) influences habitat and resource use, fitness and species' life-history strategies, ecologists have hypothesised and measured relationships between indices of habitat suitability (*i.e.* biological outcomes) and covariates predicted to influence these outcomes. Fretwell and Lucas (1969) and Fretwell (1972) equated suitability among habitats to the capacity of habitats to promote fitness of individuals relative to variation in density of coexisting individuals. Theoretically, in a state of "ideal-free distribution" of animals, fitness prospects should decrease with increasing intra- and interspecific density of and competition among co-existing organisms and ancillary negative interactions (Fretwell & Lucas 1969; Fretwell 1972). Alternative models have been proposed and tested (*e.g.* ideal despotic model, Fretwell 1972; ideal pre-emptive model, Pulliam & Danielson 1991), but support for these and others has been inconsistent (Kaminski & Prince 1981; Rosenzweig 1985; Kaminski & Gluesing 1987; Pöysä 2001). Thus, researchers have cautioned that positive associations between indices of habitat suitability and population density should not be inferred without supporting data on biological outcomes (Van Horne 1983; Kaminski & Gluesing 1987; Kaminski & Weller 1992; Elmberg *et al.* 2006; Ayers *et al.* 2013).

Habitat use and selection vary seasonally, especially for migratory species. Anderson and Batt (1983) stated: "Obviously, a comprehensive understanding of ecology and evolutionary relationships of any species requires an appreciation of selective forces that act upon individuals of it during all seasons and throughout its range." During most of the 20th century, research conducted to understand ecology and habitat use of waterfowl has focused on the breeding grounds and season (Batt *et al.* 1992; Kaminski & Weller 1992; Baldassarre & Bolen 2006). However, since the 1970s, ecologists have recognised and investigated the importance of biological events experienced and habitats and resources used by waterfowl throughout the birds' annual cycle and range (*e.g.* Weller 1975; Fredrickson & Drobney 1979; Heitmeyer & Fredrickson 1981; Kaminski & Gluesing 1987; Tamisier & Dehorter 1999; Baldassarre & Bolen 2006). Nevertheless, ecology and habitat use of vernal and autumnal staging waterfowl remain understudied compared to other seasonal sectors of the annual cycle (Arzel *et al.* 2006). Nonetheless, increased knowledge of waterfowl ecology throughout their annual cycle and range has been paramount in shaping waterfowl habitat conservation plans in North America and Europe (Canadian Wildlife Service & U.S. Fish and Wildlife Service 1986; U.S. Department of Interior, Environment Canada, & Environment and Natural Resources, Mexico 2012; Kadlec & Smith 1992; Baldassarre & Bolen 2006; Elmberg *et al.* 2006).

As researchers continue studies of waterfowl habitat use and selection, they would be wise to heed concerns and advice of Jones (2001). To paraphrase Jones (2001), "… ornithologists tend not to consistently evaluate the behavioural and fitness contexts of their findings. That can be ameliorated by recognizing that (1) habitat selection refers to a process (by individuals) and perhaps less so a pattern, (2) that there are many extrinsic factors that influence habitat selection, and (3) that a complete test of habitat selection involves an assessment of whether or not the documented habitat preferences are adaptive. A second concern was that ornithologists do not consistently use habitat-related terminology. That lack of consistency can be remedied by providing operational definitions to limit misunderstanding. A third concern was that methodologies commonly employed to document habitat selection do not account for the hierarchical nature of habitat selection and do not generate accurate representations of habitat availability. Comparisons of used habitat with available habitat are more appropriate than comparisons of used and unused habitats. Definitions of habitat availability ought to be informed by the natural and life-history characteristics of the species."

Given this background, the papers following in this section of the journal, which were presented during the 6th North American Duck Symposium, "Ecology and Conservation of North American Waterfowl," in Memphis, Tennessee in January 2013, will synthesise knowledge on habitat and resource use and selection across ducks, geese and swans, when possible, throughout the birds' annual cycle and range, focusing primarily on published studies conducted in Nearctic and Palearctic ecozones. The synthesis is organised cross-seasonally to understand carry-over biological effects related to individual fitness and population dynamics in the following sequence: 1) autumn migration and wintering habitats, 2) spring migration and pre-breeding habitats, 3) nesting habitats, and 4) post-breeding and moulting habitats. Additionally, authors will identify new questions deserving future research and suggest how advances in technology and analytical approaches may enhance understanding of waterfowl habitat use and selection. Finally, the synthesis of empirical information will be used to recommend future scientific investigations and strategies for habitat and population conservation, to help sustain harvestable populations of waterfowl and to protect rare species in the northern hemisphere amid global changes in climate, landscape, economics, socio-politics and human population growth. As we have increased our knowledge of waterfowl of the northern hemisphere throughout their annual cycle and range during the 20th and early 21st centuries (*e.g.* Batt *et al.* 1992; Baldassarre 2014), the future is rich in opportunities for collaboration of scientists and managers to advance our understanding and conservation of Anatidae and their habitats worldwide.

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