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Behavioural cues surpass habitat factors in explaining prebreeding resource selection by a migratory diving duck





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Keywords: Aythya affinis Conspecific attraction Fidelity philopatry Public information Resource utilization function Prebreeding habitat selection in birds can often be explained in part by habitat characteristics. However, females may also select habitats on the basis of fidelity to areas of previous reproductive success or use by conspecifics. The relative influences of sociobehavioural attributes versus habitat characteristics in habitat selection has been primarily investigated in songbirds, while less is known about how these factors affect habitat selection processes in migratory waterfowl. Animal resource selection models often exhibit much unexplained variation; spatial patterns driven by social and behavioural characteristics may account for some of this. We radiomarked female lesser scaup, Aythya affinis, in the southwestern extent of their breeding range to explore hypotheses regarding relative roles of habitat quality, site fidelity and conspecific density in prebreeding habitat selection. We used linear mixed-effects models to relate intensity of use within female home ranges to habitat features, distance to areas of reproductive success during the previous breeding season and conspecific density. Home range habitats included shallow water (<118 cm), moderate to high densities of flooded emergent vegetation/open water edge and open water areas with submerged aquatic vegetation. Compared with habitat features, conspecific female density and proximity to successful nesting habitats from the previous breeding season had greater influences on habitat use within home ranges. Fidelity and conspecific attraction are behavioural characteristics in some waterfowl species that may exert a greater influence than habitat features in influencing prebreeding space use and habitat selection within home ranges, particularly where quality habitat is abundant. These processes may be of critical importance to a better understanding of habitat selection in breeding birds.

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Habitat selection is one of the most fundamental aspects of ecology. A common approach within wildlife ecology is to explore relative space use by individuals based on structural and compositional aspects of habitat. Relating home range (second-order selection, sensu Johnson, 1980) and within-home-range patch (third-order) selection to habitat attributes provides basic information on a species' habitat needs. A key assumption is that individuals can identify habitat quality; habitats of high use should therefore represent high-quality habitats because individuals will recognize conditions that optimize their survival and fitness (Block & Brennan, 1993).

However, resource use is not driven solely by habitat characteristics. Individuals may respond to nonenvironmental cues that influence how they perceive available habitat (Jones, 2001). The presence of conspecifics or heterospecifics may influence the selection of habitat patches by individuals. For example, conspecific attraction has been repeatedly shown to influence territory selection in songbirds (black-capped vireo, Vireo atricapilla: Ward & Schlossberg, 2004; Baird's sparrow, Ammodramus bairdii: Ahlering, Johnson, & Faaborg, 2006; golden-cheeked warbler, Setophaga chrysoparia: Farrell, Morrison, Campomizzi, & Wilkins, 2012). Individuals could benefit from conspecific cueing if it indicates prior success in a habitat patch. Such 'public information' can play an important role in the ability of the individual to gather information about habitat quality quickly and efficiently (Danchin, Heg, & Doligez, 2001). High densities or presence of conspecifics might reveal optimal foraging patches or simply provide increased access to mates (Campomizzi et al., 2008). Congregations might

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also imply familiarity with a habitat patch, where experienced birds have had previous foraging or reproductive success, and 'naïve individuals' might rely more heavily on conspecific density as a cue (Danchin et al., 2001; Muller, Stamps, Krishnan, & Willits, 1997). Yet, conspecific cues do not necessarily indicate quality habitat; individuals may select suboptimal habitat due to the presence of conspecifics in a neighbouring territory or habitat patch (Arlt & Pärt, 2007; Betts, Hadley, Rodenhouse, & Nocera, 2008; Stamps, 1988). Such behaviour is important to consider when studying habitat selection because it can introduce perplexing variation in spatial distributions of animals (Beauchamp, Bélisle, & Giraldeau, 1997), thereby complicating efforts to link space use to habitat factors (Miller, Fletcher, & Gillespie, 2013).

Philopatric behaviour can similarly influence spatial variability in habitat selection. In migratory birds, fidelity to breeding areas and nesting sites is a common phenomenon thought to result in higher fitness of individuals (Anderson, Rhymer, & Rowher, 1992; Greenwood & Harvey, 1982). American robins, Turdus migratorius, and brown thrashers, Toxostama rufum, return more frequently to previously successful nest sites than they do to failed nest sites (Haas, 1998). Red-backed shrikes, Lanius collurio, are less likely to disperse from breeding sites where more fledglings have been produced than they are from sites with lower success (Pasinelli, Müller, Schaub, & Jenni, 2007). Evidence for philopatric behaviour also exists for migratory waterfowl, where female fidelity is positively influenced by nesting success in the previous year in common pochards, Aythya ferina, and northern shovelers, Anas clypeata (Blums, Nichols, Hines, & Mednis, 2002), and successful mallard. Anas platvrhvnchos, females nest closer to previous nest sites than unsuccessful females (Lokemoen, Duebbert, & Sharp, 1990).

Considerations of social and philopatric behaviour are critical to understanding the interactions between a species and its environment. Studying the effects of habitat factors on animal distributions may not be effective in identifying species habitat requirements without accounting for behaviours that are not directly related to physical habitat characteristics. Models that exclusively make use of physical habitat variables may lack explanatory power and predictive ability, particularly with regard to social species (Campomizzi et al., 2008; Folmer & Piersma, 2012). In resource selection studies, behavioural factors are often overlooked in groups of species such as migratory waterfowl that are well known for exhibiting strong social and philopatric behaviour. Evidence suggests that these behaviours may influence breeding and nest site selection (Coulton, Clark, Wassenaar, Howerter, & Anderson, 2011; Pöysä, Elmberg, Sjöberg, & Nummi, 1998; Ringelman, Eadie, & Ackerman, 2012).

We assessed the relative influences of both habitat attributes and sociobehavioural attributes in prebreeding resource selection of lesser scaup, Aythya affinis, females in southwestern Montana, U.S.A. Lesser scaup (hereafter, scaup) are gregarious and philopatric, and they nest later than most North American waterfowl (Austin, Custer, & Afton, 1998). Reproductive success may be heavily influenced by prebreeding habitats for scaup. Local resources contribute significantly to lipids (Cutting et al., 2013; Warren & Cutting, 2011) and protein (Cutting et al., 2011) in scaup eggs at our study site, and body condition during the prebreeding period is positively related to mean clutch size for scaup females (Warren, Cutting, & Koons, 2013). Habitat use and selection during the prebreeding period should maximize the quality and efficiency of foraging, providing an opportunity for a female to improve her body condition and chances of reproductive success. In addition, cues from conspecifics and from previous success (e.g. successful nest locations) may reinforce habitat selection by providing beneficial information to females during the prebreeding season. Because of these characteristics, scaup are an ideal study species for

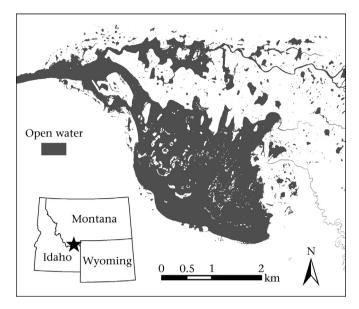


Figure 1. Project study area: Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, U.S.A. Study area extent includes all area within the figure frame.

exploring the roles of habitat attributes, conspecific densities and site fidelity during a critical life history stage.

HYPOTHESES AND PREDICTIONS

Our hypotheses of individual response to habitat characteristics were based largely on differences in habitat attributes that influence foraging opportunities for scaup. Scaup forage in open water zones of shallow wetlands and lakes (Siegfried, 1976), feeding on aquatic plant seeds and macroinvertebrates (i.e. amphipods and molluscs) during the prelaying period (Cutting et al., 2013; Krapu & Reinecke, 1992; Strand, Chipps, Kahara, Higgins, & Vaa, 2008). Torrence and Butler (2006) observed that scaup consistently forage in 50-150 cm of water during prebreeding. Scaup respond positively to open water and emergent vegetation interfaces (Murkin, Murkin, & Ball, 1997), perhaps due to greater invertebrate abundance at these locations (Voigts, 1976). We expected submerged aquatic vegetation cover to influence scaup foraging patterns, due to presumed higher densities of invertebrates (Krull, 1970) and plant seeds. Thus, we hypothesized female scaup prebreeding habitat utilization would be positively related to increasing (1) proportion of open water, (2) water depth, (3) canopy cover of submerged aquatic vegetation and (4) open water/emergent vegetation edge.

We also predicted that patterns of space use by scaup would be partially explained by sociobehavioural factors (i.e. public information and fidelity to previously successful nesting locations). Scaup breeding home ranges often overlap each other, and pairs allow conspecifics within 1–2 m (Austin et al., 1998). Conspecific attraction may influence prebreeding densities, where pairs or groups serve as indicators of foraging opportunities, safety from predators, or the presence of potential mates (Campomizzi et al., 2008; Muller et al., 1997). Group size is generally negatively related to vigilance rates (Lazarus, 2003), reducing the overall time an individual is alert and increasing the time available for foraging. This may be particularly important during the prebreeding period when waterfowl accrue significant somatic reserves for reproductive activities (Alisauskas & Ankney, 1992). We postulated that scaup would respond positively to the presence of conspecifics during the prebreeding period, as conspecific cueing and public Download English Version:

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