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

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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 ($\leq$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 platyrhynchos*, 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
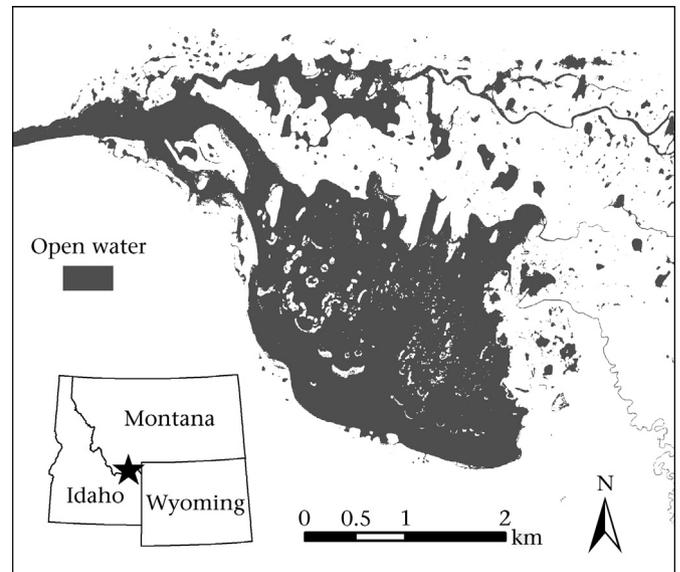

Figure 1. Project study area: Lower Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana, U.S.A. Study area extent includes all area within the figure frame.

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

information may be beneficial to social species (Danchin et al., 2001). In addition, inexperienced (younger) birds may be more likely to rely on conspecific cues to identify habitat quality or potential mating opportunities (Doligez, Cadet, Danchin, & Boulinier, 2003; Muller et al., 1997; Nocera, Forbes, & Giraldeau, 2009). Thus, we hypothesized that individual prebreeding habitat utilization would be positively correlated with increasing densities of conspecifics and that the effect would be more pronounced for younger individuals. Proximity to a birthplace or previously successful nest site might also explain spatial patterns in habitat use prior to and during the breeding season. Natal and reproductive fidelity has been reported for female scaup (Anderson et al., 1992), so we expected habitat utilization to be higher in open-water habitats near prior-year successful nesting areas.

METHODS

Study Area

We conducted our study in southwestern Montana, U.S.A., within Red Rock Lakes National Wildlife Refuge (hereafter the Refuge; Fig. 1). The Refuge encompasses approximately 10 000 ha of natural and created montane wetlands at an elevation of 2015 m, providing reproductive and migratory habitat for a diverse waterbird community. The study was conducted on Lower Red Rock Lake, a 2332 ha wetland complex comprising equal areas of shallow (<2 m) open-water and palustrine emergent vegetation habitats. The wetland supports some of the highest densities of breeding scaup in North America, with more than 7.7 pairs/km^2 (Cutting, 2010). The southwestern half of the complex is predominantly open-water habitat with interspersed islands of bulrush (*Schoenoplectus acutus*). The north and east extent of the complex is palustrine emergent vegetation (*Carex* spp.) with small (<2 ha), scattered, open-water ponds. The average annual precipitation is 49.5 cm, with 27% occurring during May and June, and the mean annual temperature is 1.8 °C. In relation to growing season length, the study site has one of the harshest and most variable breeding season environments used by scaup (Gurney et al., 2011).

Data Collection

Females were captured shortly after arrival on the breeding grounds via night-lighting from a motorboat (Lindmeier & Jessen, 1961). Age class (1–2 years old and ≥3 years old) was estimated from eye colour (Trauger, 1974) and pairing status (lone/paired/unknown) was recorded. Each female was fitted with a uniquely identifiable nasal marker comprising a combination of nylon pieces (≤14 × 14 mm) attached through the nares using 1.6 mm 316L stainless-steel welding wire and stainless-steel washers (Lokemoen & Sharp, 1985). One-third to one-half of females captured each spring ($N = 29$ in 2007, $N = 33$ in 2009) were radiomarked with implantable very-high-frequency (VHF), 19 g transmitters (19.3 × 37.3 mm) with a 22 cm (1.2 mm diameter) whip antenna (model A2310, Advanced Telemetry Systems, Isanti, MN, U.S.A.). Surgical implantation was performed following procedures from Mulcahy and Esler (1999) as modified from Korschgen, Maxson, and Kuechle, (1984). Females were released within 18 h of capture; female temperature, heart rate and respiration were monitored during surgery. Each female was released after surgery once her temperature, heart rate and respiration were determined to be stable (≤3 h after completion of surgery). Capture, handling and marking procedures were approved by Montana State University's Institutional Animal Care and Use Committee (permit number 05-07), and conducted under approved federal (MB090410-2) and state (number 2009-050) scientific collector's permits.

Vehicle-mounted, null-peak telemetry systems were used to triangulate radiomarked females 5–6 days per week (White & Garrott, 1990). Approximately 75% of daily locations were obtained between 0600 and 1300 hours, with the remaining locations obtained between 1300 and 2100 hours. Multiple bearings taken within 10 min of each other were used to map locations on hard copy aerial images of the study site. Locations were then digitized in a Geographic Information System (GIS; ArcGIS 9.3, Esri Inc., Redlands, CA, U.S.A.). This telemetry system had a mean ± SD bearing error of 0.5 ± 3.2° (Rotella, Devries, & Howerter, 1995), and triangulations of known-location transmitters placed on the ground were used to calibrate systems weekly. Telemetry locations were recorded at least 1 h apart and assumed spatially independent (White & Garrott, 1990), as individual movements for ducks can span multiple home ranges during this period. Visual observations of females were obtained up to six times weekly using hand-held three-element Yagi antennas. Incidental observations of females were recorded as well. Only locations from the prebreeding period (5 days after radiomarking through median nest initiation) were used in this analysis. No nests of marked birds were found prior to median nest initiation in either year.

We used data from nasal-marked birds to estimate the density of conspecific females during the prebreeding period. We conducted resight surveys of nasal-marked females without transmitters each year during mid-May; 72, 90, 81 and 90 females were nasal-marked during the spring of 2005, 2006, 2007 and 2008, respectively. The study site was divided into 16 survey blocks of 750 × 750 m that were each visited twice. Surveys were conducted for 4 h beginning at sunrise and 4 h prior to sunset. If a block was surveyed in the morning during the first visit, it was visited in the evening on the second visit and vice versa. Unique locations of each nasal-marked female were recorded (±75 m).

We used nest fate data to estimate nesting productivity. Nest searches were conducted in *Carex*-dominated habitats around Lower Red Rock Lake to locate nests during the summers of 2006 and 2008. Beginning in early June, investigators used behavioural observations of females to locate nests. Additional nests were located opportunistically. All nests found were marked with a flagged stick placed 4 m north of the nest bowl, and their Universal Transverse Mercator (UTM) position recorded. Nests were revisited every 6–10 days until fate was determined (≥one egg hatched or the nest destroyed/abandoned).

Utilization Distribution Home Ranges

We calculated utilization distributions (UDs; Millspaugh et al., 2006) using likelihood cross-validation smoothing for each individual in Animal Space Use 1.3 (Horne & Garton, 2009). The UD describes an animal's use of space via a probability density and can be constructed from individual locations gathered over time (Worton, 1989). UDs can be used to relate space use to resources by providing a continuous measure of an animal's relative density throughout the study area; thus, probability or intensity of use can be derived at any given location (Millspaugh et al., 2006). The likelihood cross-validation smoothing algorithm provides UD estimates with better fit and less variability given small sample sizes (Horne & Garton, 2006). We used Home Range Tools (Rodgers, Carr, Beyer, Smith, & Kie, 2007) to generate prebreeding fixed kernel density UDs and delineate 95% isopleths for home ranges (Demers, Takekawa, Ackerman, Warnock, & Athearn, 2010). A minimum of 10 locations is often needed for accurate home ranges (Börger et al., 2006). Although we could not identify a trend between home range size (ha) and the number of locations used, graphical analysis

of regression model residuals indicated that variance in home range size stabilized at approximately 15 point locations. Similarly, ordinary least squares regression indicated no relationship between home range size and number of locations for individuals with at least 15 locations ($\hat{\beta} = -56.5$, $N = 35$, $P = 0.42$), so we created a UD for each female with at least 15 locations on the study site during the prebreeding period. Individuals with more than 25% of locations occurring outside the study area were excluded from analyses. Significant outliers, identified as points located further than two standard deviations from the mean centre of telemetry locations for an individual, were assumed to result from spurious signals (White & Garrott, 1990) and thus were excluded.

Habitat Attribute Layers

Habitat layers included percentage of open water, water depth, density of open water/emergent vegetation edge and percentage of bare substrate (i.e. 100% minus the percentage of submerged aquatic vegetation canopy cover). All habitat layers were created in GIS with initial 20 m grid cells. We used National Agricultural Imaging Program (NAIP) aerial orthoimagery to create open water and edge density layers. Areas of open water were extracted from the aerial image with a histogram density slice of the near-infrared (NIR) band. Water is highly absorbent of NIR radiation relative to other features (McFeeters, 1996), making accurate identification of water possible at the pixel scale. We reclassified NAIP imagery to land/emergent vegetation and open water and calculated the percentage of open water and edge density for each cell. Edge density was the line density per cell ($km \times km^{-2}$) of the interface between open water and emergent wetland vegetation using GIS.

A bathymetric map was created from water depths (± 1 cm) taken at systematically placed point locations using a GPS unit and steel measuring tape. Depths were also gathered each summer during submerged aquatic vegetation surveys. Depths for scattered ponds adjacent to Lower Red Rock Lake were only available for a subset ($N = 16$) of ponds, so we extrapolated to unvisited ponds using a linear transform (Lyzenga, 1978) of the ratio of NIR values to visible light values (NAIP band 4/NAIP band 1:3). Depth values were adjusted depending on the mean lake water level during the prebreeding periods of 2007 and 2009. Lake depth layers for each year were interpolated from depth points using inverse-distance weighted (IDW) interpolation in GIS (radius = 200 m, minimum neighbours = 3).

Submerged aquatic vegetation surveys were conducted during the breeding season each year at random 5×5 m plots. Submerged aquatic vegetation and bare substrate cover classes were recorded at each plot (Daubenmire, 1959). We interpolated the survey data with IDW (radius = 200 m, minimum neighbours = 3) to create a percentage of bare substrate layer for each year.

Sociobehavioural Attribute Layers

We developed spatial layers to represent use by conspecifics and distance to successful nesting areas from the previous breeding season. For each year we estimated a population-level UD with a fixed kernel density estimator, using pooled locations ($N = 93$ in 2007, $N = 97$ in 2009) of nasal-marked females ($N = 58$ in 2007, $N = 63$ in 2009) observed during May resight surveys. UD estimates of nasal-marked birds were drawn from a sample independent of the telemetry study.

We generated a polygon layer in GIS for each year representing high apparent nesting density of scaup (≥ 3 nests/km^2) during the previous nesting season. Apparent nesting density was based on the number of nests found during searches uncorrected for detection probability. From this layer, we eliminated polygons without

successful nests. Remaining polygons represented areas of nesting productivity. For each study year, we calculated a Euclidian distance raster in GIS representing the distance from each cell in the study site to the prior year's successful nest polygons. Maximum distances exceeded 2000 m, so we standardized this variable for analysis.

Resource Utilization Functions

UDs for each bird were clipped to the 95% isopleth that we defined as an individual's home range. Grid cells for each habitat attribute layer were set to the exact spatial extent of the home range layer; UDs and spatial attributes for each individual bird were then averaged within 100 m cells in the Geospatial Modelling Environment (Beyer, 2012). We estimated the influence of spatial habitat and sociobehavioural attributes on each log-transformed UD using linear mixed-effects models in R (R Development Core Team, 2012) package 'nlme' (Pinheiro, Bates, Debroy, Sarkar, & R Development Core Team, 2011). Random effects helped account for the variance structure imposed by repeatedly sampling from an individual female's home range (Hebblewhite & Merrill, 2008). Additionally, mixed-effects models provided flexibility in accounting for residual error correlation and nonconstant variance among groups (Pinheiro & Bates, 2000).

We took a sequential modelling approach to explain variation in female habitat selection to simplify model complexity and reduce the number of models considered. This strategy was useful because we could not compare all possible models using purely information-theoretic methods (e.g. Stephens, Buskirk, Hayward, & Del Rio, 2005); such an approach would have resulted in more than 100 potential model fits based on the number of explanatory variables alone. First, we determined an appropriate functional form for edge density and distance to prior year successful nests based on our a priori hypotheses. Linear, quadratic and pseudothreshold functional forms (Franklin, Anderson, Gutiérrez, & Burnham, 2000) were considered as candidate models for these attributes with individual as a random effect. The top functional form was determined using Akaike's Information Criterion, AIC (Burnham & Anderson, 2002). All other spatial attributes were assumed to take linear forms and/or include interactions. We did not consider models with collinear variables (Pearson's $r > 0.7$). All spatial attributes, age class and year were included as fixed effects in a full model with individual as a random effect. An interaction between age class and conspecific density was included to test for a difference in response to the presence of conspecifics between young and more experienced females. We also included an interaction between water depth and year to help explain variation in female selection with differences in water levels between years. We refitted the full model using each of the spatial correlation structures available in R package 'nlme' (linear, spherical, exponential, Gaussian and rational quadratic; Pinheiro & Bates, 2000). The best residual error correlation structure was determined from semivariograms and confirmed with AIC values (Pinheiro & Bates, 2000); this structure was then included in our full model. We removed insignificant variables using likelihood ratio tests (LRTs) until the best fit was achieved (Zuur, Ieno, Walker, Saveliev, & Smith, 2009); LRT results were confirmed by ΔAIC scores >2. The resultant model was tested for lack of fit by plotting normalized residuals (see Pinheiro et al., 2011) against fitted values to investigate patterns indicating a violation of independence. Nonconstant variance associated with age class and year was explored with residual plots. Variance weights for year were included to accommodate remaining heteroscedasticity (Zuur et al., 2009). We explored the relative influence of each predictor in turn by extrapolating its partial regression coefficient across its full range of

predictor values (see Results, Figs 2, 3). Confidence intervals for these estimates were calculated with the delta method (Bolker, 2008).

RESULTS

Females were captured and radiomarked during 12–16 May 2007 ($N = 29$) and 23–27 May 2009 ($N = 33$). Prebreeding home ranges were created for 21 females in 2007 and 14 females in 2009. Home ranges were generated using 15–41 locations per bird. Of the 35 females studied, 17 were classified as 1–2 years old and 18 as ≥ 3 years old; 32 females were paired at capture, two were alone, and pairing status was unknown for one individual.

The study area (Fig. 1) included all flooded sedge, ponds and lake within the Lower Red Rock Lake complex, 95% of prebreeding locations, 836 ha of open water, and 1396 ha of emergent vegetation (i.e. flooded sedge, bulrush island, dry sedge); we defined this area as available habitat. Annual precipitation for the 2007 water year was 13 cm below the 30-year average (1979–2009), 30% of which fell after the prebreeding period. In contrast, 2009 precipitation was 0.3 cm below average. Lake water levels reflected this difference, as 2007 was characterized by lower water depths and exposed mud flats during the prebreeding period. Mean $\pm$ SD depths for open water were 46.9 ± 17.5 cm in 2007 and 61.3 ± 18.9 cm in 2009, and the mean percentage of bare substrate was $40.5 \pm 29.3\%$ in 2007 and $31.3 \pm 25.2\%$ in 2009. The study area

included 441 km of open water–emergent vegetation edge with a mean density of 8.3 ± 17.6 km $\times$ km^{-2}.

Home Range Attributes

Home range size varied widely from 128 to 1544 ha over both years. Mean size $\pm$ SD was 522 ± 317 ha, $N = 35$ (457 ± 262 ha, $N = 21$ in 2007; 620 ± 375 ha, $N = 14$ in 2009). Female home ranges had intermediate edge densities (21 ± 4 km $\times$ km^{-2}), shallow to intermediate water depths (52 ± 10 cm) and submerged aquatic vegetation canopy covering 45–88% of home range areas. The distribution of individual UD values ranged from 0.01 to 2.75 and was positively skewed ($\bar{x} = 0.18$, median $= 0.10$, 95th percentile $= 0.6$). Mean percentage of open water ranged from 17% to 79% in home ranges (Table 1), and open water and emergent vegetation were roughly equivalent between years ($49.4 \pm 14.7\%$ and $51.6 \pm 15.1\%$ in 2007 and 2009, respectively). Mean water depths within home ranges (open water habitat only) were shallower in the drought year of 2007 (46.6 ± 7.6 cm) than in 2009 (58.5 ± 8.5 cm). Conversely, home range water depths within flooded emergent vegetation were deeper in 2007 (28.6 ± 8.1 cm) than in 2009 (17.8 ± 5.7 cm), which probably resulted from a higher proportion of flooded emergent vegetation being composed of bulrush islands. These islands were located in deeper water, while most sedge-dominated areas were dry in 2007. The amount of bare substrate in female home ranges was greater in 2007 than in 2009 ($33.5 \pm 10.5\%$ and $21.7 \pm 6.0\%$). Habitat edge was 21.8 ± 4.0 km $\times$ km^{-2} in 2007 and 19.4 ± 2.3 km $\times$ km^{-2} in 2009.

Resource Utilization Functions

The full model for habitat selection (i.e. the resource utilization function) included all independent variables. A strong positive correlation was evident between open water and depth (Pearson correlation: $r = 0.80$); therefore, we retained open water only as an indicator term for percentage of bare substrate (i.e. percentage of bare substrate only estimated where open water was present). Distance to successful nest areas and edge density demonstrated nonlinear relationships with log-transformed UD values (i.e. scaup habitat utilization). The top functional form between habitat utilization and distance to successful nest areas was quadratic (54 AIC units better), indicating that the response reached a maximum at intermediate distances to prior year successful nest areas. A pseudothreshold relationship between habitat utilization and edge density was indicated, with 50 AIC units separating this model from the next.

The semivariogram model suggested a linear spatial correlation structure with a range of 800 m (Pinheiro & Bates, 2000). A semivariogram of the normalized residuals indicated that this model accounted for spatial dependence within home ranges. All spatial attributes and tested interactions were significant predictors ($P < 0.01$) and thus were retained in the resource utilization function (Table 2). Inspection of final model residuals and QQ plots did not reveal lack of fit. Thus, our results indicated that female habitat selection was associated with both sociobehavioural attributes and habitat attributes.

Effects of habitat attributes on selection were highly significant ($P < 0.01$), but effect sizes were relatively small (Table 2). However, when considered across the range of attribute and utilization values, most effects were considered biologically significant (Figs 2, 3). Selection of edge density within the home range was an exception, with an increase of less than 0.01 in habitat utilization across the full range of edge densities used by female scaup.

The interaction between water depth and year (Table 2) suggested that the influence of water depth was considerably stronger
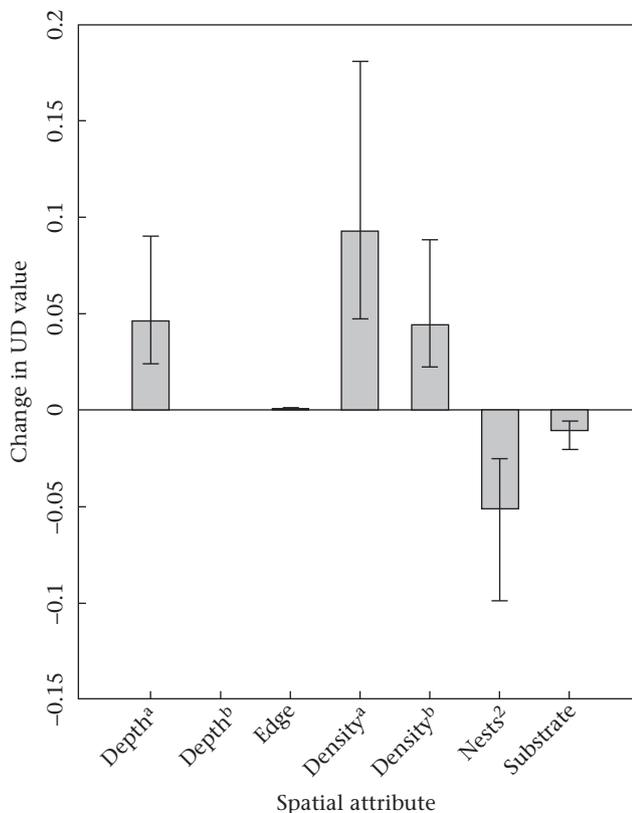

Figure 2. Estimated change in utilization distribution (UD) and 95% confidence intervals for each associated spatial attribute when extrapolated across its full range of values. Estimates were obtained and backtransformed from prebreeding female scaup resource utilization function (RUF) $\hat{\beta}$ coefficients, with uncertainty estimated from the RUF variance–covariance matrix. Depth[a]: depth effect for 2007; Depth[b]: depth effect for 2009; Edge: density (km $\times$ km^{-2}) of open water/emergent vegetation edge; Density[a]: conspecific attraction effect for individual female scaup age 1–2 years; Density[b]: conspecific attraction effect for individual female scaup age ≥ 3 years old; Nests[2]: second-order effect for increasing distance to prior year successful nest areas; Substrate: percentage bare substrate of open water.
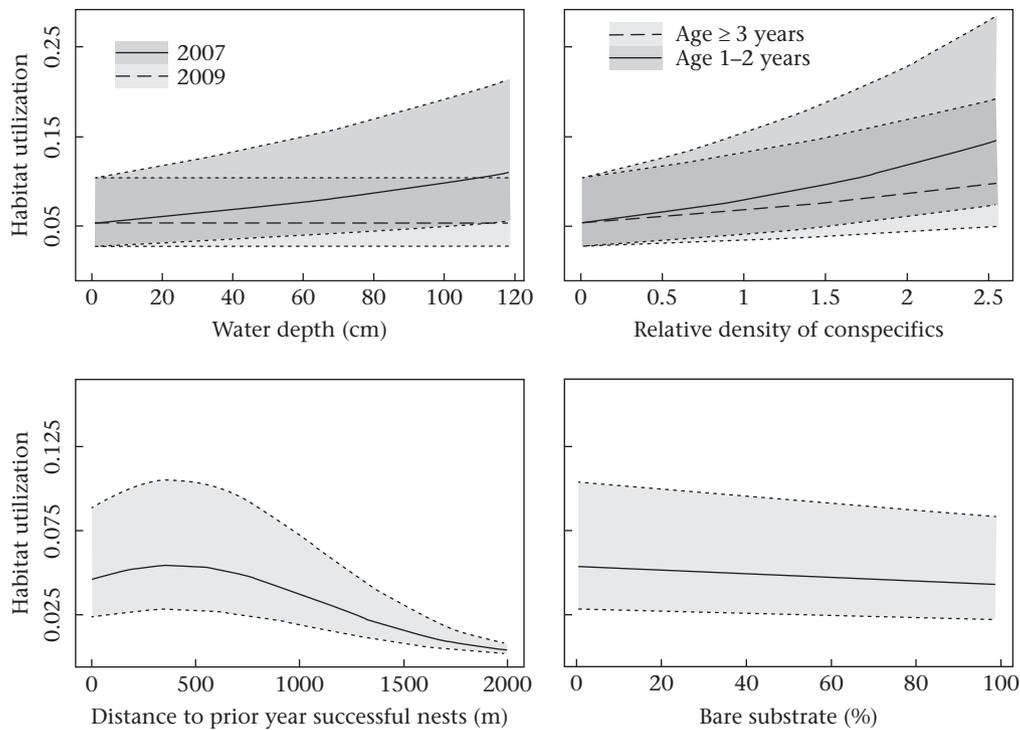
Figure 3. Relations between spatial attributes and resource utilization of female lesser scaup at Red Rock Lakes National Wildlife Refuge, Montana, U.S.A, during the prebreeding seasons of 2007 and 2009. Estimates were obtained and backtransformed from prebreeding female scaup resource utilization function (RUF) $\hat{\beta}$ coefficients, with 95% CIs estimated from the RUF variance–covariance matrix. Habitat utilization and relative density of conspecifics represent a smoothed intensity of use metric, and thus, units are not reported. Edge density was omitted from the figure due to lack of biological significance ($\hat{\beta} = 0.002$, SE < 0.001).

during the drought year 2007. Conversely, the effect was minimal for 2009 (Table 2, Figs 2, 3). Habitat utilization was negatively associated with percentage of bare substrate ($\hat{\beta}_{Substrate} = -2.2 \times 10^{-3}$, SE = 1.0×10^{-4}), supporting the hypothesis that scaup select for higher levels of submerged aquatic vegetation cover.

Habitat use peaked at intermediate distances (≈ 300 m) from prior year successful nesting areas ($\hat{\beta}_{Nests^2} = -14.3 \times 10^{-2}$, SE = 4.7×10^{-3}), reflecting selection of open-water areas near these sites (Fig. 3). A significant positive relationship was found between habitat utilization and conspecific density, and the effect differed by age class ($\hat{\beta}_{Density*age} = -15.7 \times 10^{-2}$, SE = 3.3×10^{-2}). Young females responded more strongly to conspecific density; for every unit increase in conspecific density, mean ± SE utilization of

young females increased by 48 ± 0.02%. A similar unit increase in conspecific density increased mean utilization of older females by 27 ± 0.30%. Under normal conditions (e.g. 2009), prebreeding females responded more strongly to conspecific density and distance to prior year successful nest areas than they did to habitat factors within their home ranges (Fig. 2).

DISCUSSION

Animal habitat selection is influenced by habitat structure, interactions between and among species (Campomizzi et al., 2008; Forsman, Mönkkönen, Helle, & Inkeröinen, 1998), and collective or individual experience (Blums, Nichols, Hines, Lindberg, & Mednis, 2003). Ahlering et al. (2010) reviewed conspecific cueing in songbirds and found evidence for conspecific attraction in 20 of

Table 1
Prebreeding mean home range attributes of female lesser scaup in southwestern Montana, U.S.A. in 2007 and 2009

Year	Attribute	Range	Mean	SD
2007	Area	128–1000	457	262
	Open water	17.1–74.0	49.4	14.7
	Depth of open water	27.3–64.4	46.6	7.6
	Depth of flooded emergent vegetation	19.4–44.9	28.6	8.1
	Substrate	14.4–55.0	33.5	10.5
	Edge	11.9–26.7	21.8	4.0
2009	Area	231–1544	620	375
	Open water	30.7–79.3	51.6	15.1
	Depth of open water	34.0–66.9	58.5	8.5
	Depth of flooded emergent vegetation	13.1–30.6	17.8	5.7
	Substrate	12.4–35.1	21.7	6.0
	Edge	14.8–22.8	19.5	2.3

Attributes included area (ha), percentage of open water, depth of open water (cm), depth of flooded emergent vegetation (excludes dry ground, cm), percentage of unvegetated open water wetland substrate (substrate) and open water–emergent vegetation edge density (edge, km × km^{-2}).

Table 2
Regression coefficient statistics from the resource utilization function for prebreeding female lesser scaup during 2007 and 2009 in southwestern Montana, U.S.A.

Model parameter	$\hat{\beta}$	SE ($\hat{\beta}$)	t	df	P
Intercept	−2.923	0.337	−8.675	16 513	<0.001
Depth	0.006	<0.001	21.287	16 513	<0.001
Year (2009)	0.363	0.383	0.947	32	0.351
Depth*year (2009)	−0.006	<0.001	−21.006	16 513	<0.001
Edge	0.002	<0.001	5.372	16 513	<0.001
Substrate	−0.002	<0.001	−21.572	16 513	<0.001
Nests	0.078	0.011	7.054	16 513	<0.001
Nests^2	−0.143	0.005	−30.794	16 513	<0.001
Density	0.394	0.022	18.275	16 513	<0.001
Age (≥3 years old)	0.086	0.376	0.229	32	0.821
Density*age (≥3 years old)	−0.157	0.033	−4.687	16 513	<0.001

Age: 1–2 years old vs ≥3 years old; depth: water depth; edge: log-transformation of edge density; substrate: percentage of bare substrate of open water; nests: standardized distance to successful nesting area; density: density of conspecifics.

24 studies. Ward, Benson, Semel, and Herkert, (2010) documented higher-than-expected occupancy of wetlands by a variety of wetland bird species where pied-billed grebes, *Podilymbus podiceps*, were already present, suggesting a response to cues from heterospecifics. Common goldeneye, *Bucephala clangula*, females appeared to use public information when prospecting for nests; more frequent prospecting activity was documented at active versus nonactive nests (Pöysä, 2006). While awareness of such behavioural influences on habitat selection is increasing, habitat models commonly fail to account for behavioural factors that may be indirectly related to or independent of habitat (Danchin, Giraldeau, Valone, & Wagner, 2004; Ricklefs, 2013). Such omissions likely complicate efforts to explain spatial structure in selection based on habitat or landscape heterogeneity (Campomizzi et al., 2008; Guisan et al., 2006). A potential remedy for some of these problems is to incorporate spatial autocorrelation into the model framework at an appropriate spatial scale (e.g. Folmer, Olff, & Piersma, 2012; Mattsson et al., 2013). However, this approach may be somewhat limited to clustered species, and spatial structure is often dynamic and species specific. Our findings suggest further evidence of spatial pattern in habitat selection of migratory birds being driven in part by factors that include behavioural components and/or social information.

We observed considerable overlap and wide variation in size and structure of prebreeding home ranges in female scaup. Characteristics of habitat quality alone may not explain such variation (e.g. Nocera et al., 2009), and little variation was explained by habitat variables in our resource utilization function. Structural attributes of preferred habitats may be poor predictors of selection if they are widely available, as these habitats may appear to be underutilized (Aarts, Fieberg, Brasseur, & Matthiopoulos, 2013; Garshelis, 2000). The variation that we observed in scaup home ranges could be caused by a combination of factors such as individual heterogeneity (e.g. differences in experience, body condition: Warren et al., 2013; breeding status: Martin, Lindberg, Schmutz, & Bertram, 2009; cross-seasonal effects: Anteau & Afton, 2009; patchy distribution of resources: Anderson & Titman, 1992), and/or intra- and interspecific interactions. Although we could not explore every possibility, we did find support for our hypotheses that habitat utilization is influenced by conspecific density and distance to prior year successful nesting areas. These variables had a greater effect on selection than did habitat variables under normal conditions on our study site. The ability of intra- and interspecific interactions to explain spatial variability in migratory birds is becoming more apparent (Campomizzi et al., 2008; Nocera et al., 2009) and in some cases these effects supersede those of habitat structure (Betts et al., 2008). Spatial patterns in home ranges of prebreeding scaup on our site may have been partially dependent on factors such as group behaviour and prior experience.

Habitat utilization was strongly influenced by relative densities of nasal-marked females. The spatial distribution of these birds could include information from key habitat predictors not accounted for in our resource utilization function. For example, if female scaup in the study (nasal-marked and radiomarked) were selecting for the same habitat feature, which was not accounted for in our model, then the correlation could be manifested in the presence or density of conspecifics. In this way, a missing variable (or variables) could constitute part of the disparity in overall effect sizes (e.g. Fig. 2) between habitat attributes and conspecific density. However, unexplained spatial variation is common in habitat selection modelling, and potential explanatory factors, such as pathogens or predator avoidance, may be difficult to quantify (Ricklefs, 2013). The large difference in the effect of conspecific density on younger versus older birds seems unlikely to be due to a missing habitat component, which would also have had to trigger the difference in selection between age classes. Similarly, if the effect of conspecific density is in fact representative of quality habitat, then younger and less experienced individuals seemingly would benefit more from using this cue. Such individuals may be particularly dependent upon information conveyed through conspecific presence (reviewed in Muller et al., 1997). For example, immigration rates in female mallard yearlings are related to abundance of conspecific breeding pairs (Coulton et al., 2011). In two species of grassland songbirds, first-year breeders rely more heavily on conspecific cues in habitat selection than do older individuals (Nocera et al., 2009). Young scaup females in our study demonstrated stronger selection for habitats on the basis of density of conspecifics than did older females, perhaps responding to conspecific cues to compensate for a lack of experience (see Doligez et al., 2003; Muller et al., 1997). The influence of conspecific density for young females was nearly twice that of older females (Figs 2, 3). Conspecific cueing has been observed in many bird species, including waterfowl. Presence of conspecifics may provide information to an individual about potential foraging opportunities (Pulliam & Millikan, 1982). Teal (*Anas crecca*) use the presence of conspecifics in selecting foraging patches, landing near foraging conspecifics and mimicking their feeding behaviours (Pöysä, 1987).

Females selected prebreeding habitats adjacent to prior year successful nest areas, supporting our hypothesis of female fidelity to these locations. Scaup are strongly philopatric to breeding areas (Afton, 1984; Johnson & Grier, 1988) and may be influenced by prior reproductive success, while information on the success of conspecifics could also be used as a cue (Boulinier & Danchin, 1997). Successful female mallards and gadwall, *Anas strepera*, nest within 250 m of their previous nest sites (Lokemoen et al., 1990). Strong fidelity to breeding sites has also been documented in redheads, *Aythya americana* (Arnold, Anderson, Sorenson, & Emery, 2002) and canvasbacks, *Aythya valisineria* (Anderson, Emery, & Arnold, 1997) and has been linked to quality habitat and reproductive success in northern shovelers (Blums et al., 2002). Use of public information has been suggested for goldeneye (Pöysä, 2006). The observed response to successful nest areas by scaup in our study may simply result from females selecting for good current-year nesting habitat. While this influence could cause the observed correlations, we note that the distribution of successful nests in 2006 and 2008 differed considerably in spatial extent. For example, the area representing nesting productivity in 2006 (11.1 km^2) was more than twice that of 2008 (4.8 km^2) with only 37% overlap, which could be partially attributed to a difference in water levels between the two nesting seasons. Water levels during nesting (1 June–31 July) were 16 cm higher on average in 2006 than in 2008 ($t_{112} = 17.19$, $P < 0.001$). The observed nonlinear relationship between scaup habitat utilization and prior year successful nesting areas for both study years may indicate more than a basic response to nesting habitat, which varies spatially and temporally. Nesting habitat, philopatric behaviour (breeding site fidelity) and public information could potentially interact to explain scaup habitat utilization.

Our study suggests that habitat selection in scaup females may be driven by factors beyond habitat structure within their prebreeding home range, with potential relevance for conservation and management of Anseriformes. Considerable monetary resources are directed at the conservation of breeding habitat for North American waterfowl, with approximately $13 million being spent annually in the U.S. Prairie Pothole Region alone (Niemuth et al., 2008). More than 15.7 million acres of grassland and wetland habitat have been restored or protected since 1986 in the U.S., Canada and Mexico (North American Waterfowl Management Plan, 2012). Habitat patches are often prioritized for conservation using spatially explicit models that predict density of breeding

ducks based on important habitat attributes. A key assumption of these efforts is that density of breeding ducks is positively related to the reproductive potential of a habitat patch (Niemuth et al., 2008). While this assumption remains largely untested, results from studies such as ours provide additional insights into the interpretation of models used to direct conservation. For example, prebreeding habitat selection within home ranges by females in our study was strongly influenced by proximity to areas of successful reproduction the prior year. This legacy effect of reproductive success could result in a correlation of density with reproductive potential of a habitat, albeit with a lag of at least 1 year. Thus, validity and predictive ability of conservation planning modelling approaches could be improved by a better understanding of how philopatric behaviour affects breeding bird densities.

Waterfowl likely respond to public information at multiple scales (see Pöysä, 1987; Pöysä et al., 1998). We documented potential sociobehavioural effects on habitat selection within home ranges. These effects may be easier to detect when high-quality habitat is abundant; the observed effect of water depth during a drought year in our study might imply that the importance of local-scale habitat increases when conditions are limiting. Studies of habitat selection tend to rely heavily on environmental characteristics in explaining space use. We suggest that factors indirectly related to or independent of physical habitat may be important, particularly in cases where directly measured habitat features fail to explain variation within a species home range. Additional research is needed to explore the circumstances under which behavioural influences occur in habitat selection and to identify breeding habitat features and behavioural components of selection that correlate with fitness and productivity at the individual and population levels in waterfowl. Behavioural factors such as breeding site fidelity and conspecific attraction may be influential in determining space use, and acknowledging these processes may be of critical importance to a better understanding of habitat selection in breeding birds.

Acknowledgments

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