

## CHAPTER FOUR

### Breeding Distribution and Ecology of Pacific Coast Surf Scoters

John Y. Takekawa, Susan W. De La Cruz, Matthew T. Wilson,  
Eric C. Palm, Julie Yee, David R. Nysewander,  
Joseph R. Evenson, John M. Eadie, Daniel Esler,  
W. Sean Boyd, and David H. Ward

**Abstract.** Recent declines in sea duck populations have highlighted the need for additional basic research across the life cycle of these long-distance migratory birds. A lack of basic ecological information on Surf Scoters (*Melanitta perspicillata*), including the linkage between wintering and breeding areas and description of their nesting areas, is a major impediment to determining factors contributing to their decline. We marked 415 Surf Scoters with radio and satellite transmitters at four wintering areas along the Pacific coast to describe their breeding synchrony, sympatry, philopatry, and nesting areas selection in the northern boreal forest (NBF). Their primary breeding region was located in the western NBF centered on the Great Slave and Great Bear Lakes in the Northwest Territories, Canada, and their mean settling date (31 May) was remarkably synchronous ( $\pm 0.9$  d). We developed a nearest-neighbor statistic *C* to examine nesting areas of individuals from different wintering areas and found that they were not clustered ( $C = 0.031$ ,  $P = 0.15$ ), but nests of eight individuals found in successive years

were highly philopatric and within  $1.2 \pm 0.2$  km of their previous locations. Finally, we compared nesting areas and random locations with stepwise selection in a second-order Akaike Information Criterion (AIC<sub>c</sub>) analysis to identify the best models. Key landscape features included distance to snowline, elevation gradient, numbers of lakes, distance to treeline, and latitude. A nonparametric classification and regression tree (CART) showed that nesting areas were in an arc of habitat near snowline ( $< 218$  km), in lower elevation gradients ( $< 14$  m/km), and in areas with 3–6 lakes within  $2 \times 2$  km. Climate change is predicted to have the greatest effects on more northern ecosystems, and NBF species like Surf Scoters with relatively inflexible breeding ecology may be adversely affected if they are unable to adapt quickly to rapidly changing conditions.

**Key Words:** Baja California, boreal forest, breeding, *Melanitta perspicillata*, migratory connectivity, nearest neighbor, Northwest Territories, Puget Sound, San Francisco Bay, San Quintin Bay, site fidelity, Strait of Georgia, Surf Scoter.

---

Takekawa, J. Y., S. W. De La Cruz, M. T. Wilson, E. C. Palm, J. Yee, D. R. Nysewander, J. R. Evenson, J. M. Eadie, D. Esler, W. S. Boyd, and D. H. Ward. 2011. Breeding distribution and ecology of Pacific coast Surf Scoters. Pp. 41–64 in J. V. Wells (editor). *Boreal birds of North America: a hemispheric view of their conservation links and significance*. Studies in Avian Biology (no. 41), University of California Press, Berkeley, CA.

Understanding relationships between non-breeding and breeding populations is fundamental to our knowledge of migratory bird ecology. Although many studies have examined migratory populations during wintering or breeding periods, few cross-seasonal studies have been undertaken on individual birds across these primary life-cycle stages (Webster et al. 2002). The primary reason that such research has been limited is because of the great difficulty in relocating individuals at both ends of their migratory routes. However, the development of satellite telemetry over the past decade has made such studies feasible for larger migratory birds such as waterfowl.

Information on migratory connectivity has been exceedingly sparse for sea ducks (Tribe Mergini) in North America, most of which winter in the temperate coastal waters and breed in remote sub-Arctic and Arctic regions. One species, the Surf Scoter (*Melanitta perspicillata*), breeds from Labrador to Alaska and winters along the Pacific and Atlantic coasts (Savard et al. 1998). Surf Scoters are the only scoter endemic to North America, and little is known about their breeding distribution and abundance, because this species nests in very low densities across an extensive range (Savard et al. 1998).

Surf Scoters nest in the northern boreal forest (NBF), a region characterized by extremes in temperatures and precipitation, low plant species diversity, recurring disturbances such as fire, dramatic fluctuations in insect and vertebrate populations, and sparse human populations (Shugart et al. 1972, Chapin et al. 2006). Physical and biological processes in the NBF are shaped by low temperatures and permafrost soil; organisms residing in the NBF are adapted to low temperatures (Chapin et al. 2006). The NBF has been described as a region with relatively stable wetland habitats (Jessen 1981), but in the past three decades, many areas of the NBF in western North America have warmed more rapidly than any other region on earth (Serreze et al. 2000). Sea ducks are the most northerly nesting of the ducks (Goudie et al. 1994), and climate-induced change, including alteration of wetlands (Smol and Douglas 2007), has been predicted to have the greatest effect on northern ecosystems (Soja et al. 2007).

Migratory birds such as the Surf Scoter occupy the NBF for 3–4 months of the year. Their productivity is a compromise of competing migratory schedules

(Drent et al. 2003), where a lack of resources early in the season is balanced against declining reproductive success with advancing date. Surf Scoters pair on the wintering grounds and begin laying eggs in early June. Males depart soon after egg laying while females tend broods (Savard et al. 1998). Their habitat preferences for nesting areas are not known, but the few nests that have been reported are well concealed under conifers at variable distances to open water (Savard et al. 1998).

Surf Scoters are counted annually during the breeding waterfowl surveys in May; however, scoter numbers are not well documented, because the extent and timing of the May surveys are targeted for Mallards (*Anas platyrhynchos*) and survey coverage is less extensive within the NBF than in other waterfowl breeding habitats (Smith 1995, Hodges et al. 1996). During the annual May breeding survey, the majority of Surf Scoters are found in the NBF strata. Nevertheless, long-term surveys indicate declining trends in the breeding population of Surf Scoters (Goudie et al. 1994, Hodges et al. 1996, Savard et al. 1998, Sea Duck Joint Venture 2001, USFWS 2002, Nysewander et al. 2004). The Surf Scoter population has been estimated at 536,000 breeding birds (Goudie et al. 1994), and over the past two decades, the population has decreased nearly 50% (Sea Duck Joint Venture 2001).

Coincident with the declines on the breeding grounds, the number of Surf Scoters wintering in Pacific coast estuaries also has declined over the past two decades (USFWS 2002, Nysewander et al. 2004). These wintering areas face a variety of anthropogenic threats, such as contaminant exposure, nonnative species invasions, aquaculture, physical habitat alteration, and disturbance (Nichols et al. 1986, Carlton et al. 1990, Cohen and Carlton 1995, Savard et al. 1998, Linville et al. 2002, Nysewander et al. 2004). A lack of basic ecological information on Surf Scoters, including the linkage between wintering and breeding areas and description of their nesting areas, is a major impediment to determining factors contributing to their decline.

In this study, we integrated results from Surf Scoters marked with satellite transmitters at four wintering areas along the Pacific coast. We documented the scope of their core breeding area, their nesting synchrony and site fidelity, and the level of connectivity of wintering and breeding areas. Finally, we examined landscape features of the NBF to determine if Surf Scoters selected

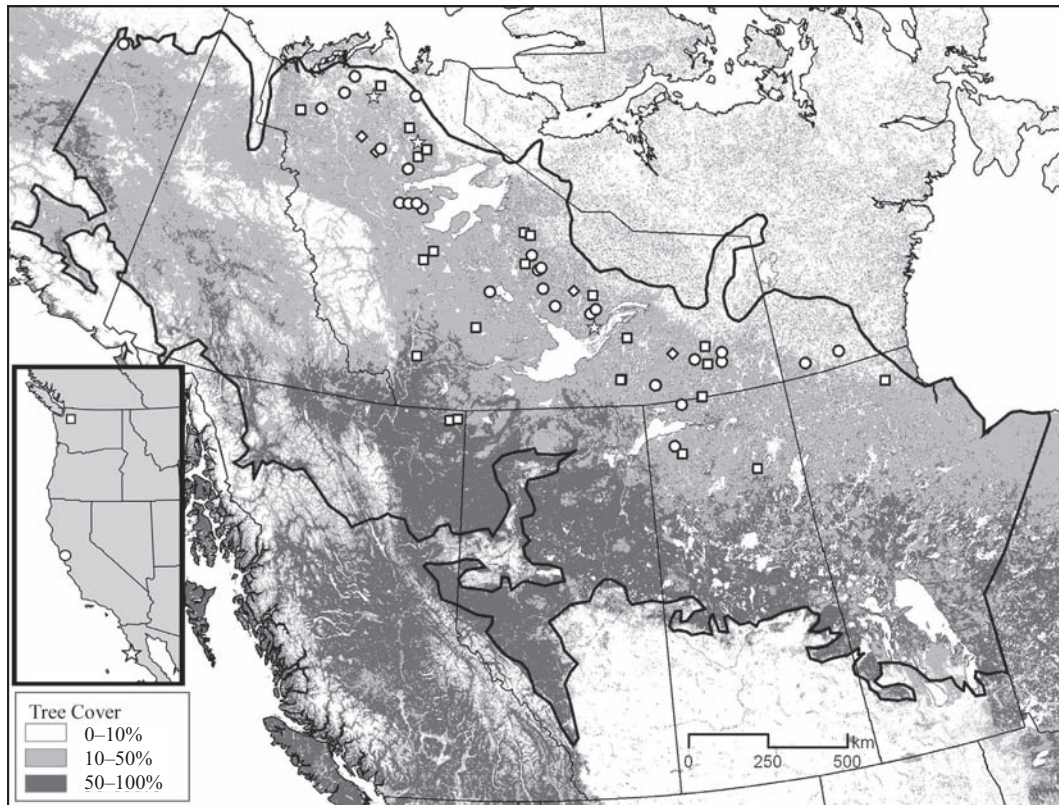


Figure 4.1. Outline of the breeding range extent for Surf Scoters in the northern boreal forest from eastern Alaska to the Ontario border, where shading indicates percent tree cover. Symbols show breeding locations for nesting Surf Scoters from different wintering areas, including San Quintin Bay, Baja California, Mexico (SQ, star); San Francisco Bay, California, USA (SF, circle); Puget Sound, Washington, USA (PS, square); and Strait of Georgia, British Columbia, Canada (SG, diamond). Inset shows four wintering areas where Surf Scoters were captured and marked.

specific areas for nesting, and how predicted climate-induced changes in the NBF may affect their breeding ecology.

## METHODS

### Study Area

The wintering range of Surf Scoters on the Pacific coast extends from Alaska to Baja California, Mexico (Savard et al. 1998). We compiled information from studies of Surf Scoters captured and marked at four wintering areas along the Pacific coast (Fig. 4.1). The wintering area name, coordinates, and approximate distance of their migration route to the breeding grounds (De La Cruz et al., 2009) included San Quintin Bay, Baja California, Mexico (SQ: 116.0°W, 30.4°N; 4,500 km), San Francisco Bay,

California, USA (SF: 122.4°W, 37.8°N; 3,750 km); Puget Sound, Washington, USA (PS: 122.4°W, 47.5°N; 2,000 km); and the Strait of Georgia, British Columbia, Canada (SG: 122.4°W, 49.3°N; 2,500 km). We examined landscape features within the breeding distribution of Surf Scoters in the NBF region of western Canada and eastern Alaska. We used tree density data from a digital coverage of the NBF (E. Butterworth, pers. comm.) georeferenced in ArcMap v. 9.2 (ESRI Inc., Redlands, CA) to delineate the southern extent of available nesting habitats and the treeline coverage for the northern extent. On the basis of our preliminary fieldwork and the satellite transmitter data in 2003, we defined longitude 148°W in eastern Alaska as the western boundary and the Manitoba–Ontario border (~95.2°W) as the eastern boundary of the breeding range for our analyses (Fig. 4.1).

## Capture and Marking

We captured 415 Surf Scoters on their wintering grounds between November and March 2002–2006 with floating mistnets (Kaiser et al. 1995) or a net shot from a netgun on a fast-moving boat. Each bird was sexed and aged, banded, and measured. Selected individuals were abdominally implanted (Korschgen et al. 1996) with a platform-transmitter-terminal (PTT) satellite transmitter or very-high-frequency (VHF) radio transmitter with an external antenna. A study comparing different attachment methods (Iverson et al. 2006) concluded that this type of coelomic implant provides reliable, unbiased telemetry location data. Marked birds were released after a recovery period of at least two hours. VHF transmitters provided a signal every 1–2 sec for the life of the transmitter, while PTT transmitters had duty cycles to record location data for 6–8 h and off for 48–96 h, depending on the seasonal programming for the different project objectives.

## Nesting Locations

Nesting locations of Surf Scoters were determined primarily from birds marked with satellite transmitters. Locations were obtained from the Argos data system, which estimated positions by calculating the Doppler-effect shift with receivers on National Oceanic and Atmospheric Administration (NOAA) polar-orbiting weather satellites. In 2003, 2005, and 2006, nesting locations were supplemented from extensive aerial searches of Surf Scoters marked with VHF transmitters. Observers used 1–2 receivers to listen and locate marked individuals as they flew in fixed-wing aircraft (Cessna 185 or 206) from Yellowknife (114.3°W, 62.5°N) outfitted with dual four-element Yagi antennas on their wing struts. Telemetry flights were flown in a grid pattern over most of the NBF in the Northwest Territories from Inuvik to the Alberta border and from the MacKenzie River in the west to treeline in the east. The initial, extensive aerial searches were conducted at higher elevations (>1,500 m) with an estimated detection range of 50 km for a total strip width of 100 km. Subsequent intensive searches were conducted at lower elevation (<800 m), focused on a core area (300 km × 900 km) between the Great Slave and Great Bear Lakes.

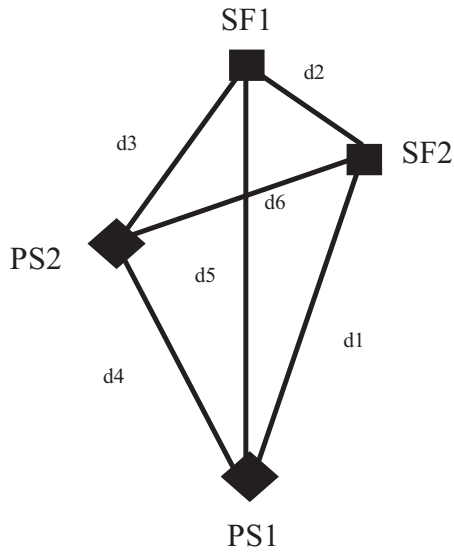
For this analysis, we compiled the location data from all of the PTT-marked Surf Scoters and removed those with Argos location quality (LQ)

classes of 0 (<1,500 m error), A, B, or Z (error not estimable). Although field comparison studies indicate that accurate locations are obtained for a large proportion of locations in these lower LQ classes (see Miller et al. 2005), we used a conservative approach to describe the breeding distribution by analyzing only those locations with Argos LQ codes of 1 (<1,000 m), 2 (<350 m), or 3 (<150 m). We discarded locations that were separated by less than an hour, since an hour was sufficient time for a scoter to cross its breeding home range, thereby reducing potential autocorrelation (White and Garrott 1990).

The center of the nesting area for each bird was determined in ArcMap with the “mean center” tool in ArcToolbox. The distance from each location to the mean center was calculated with Hawth’s Tools (Beyer 2004), and outliers more than two standard deviations from the mean were deleted (<4% of the data). The remaining data were used to estimate nest site locations for habitat analyses. Five Surf Scoters had bimodal distributions that may have represented two nesting attempts in separate areas; for these cases, we used the first cluster of locations for the analyses. Locations were placed into 2 × 2 km or 4 × 4 km grids (UTM Zone 10, NAD83; ArcMap Fishnet Tool; ESRI 1996) that covered the breeding range for our habitat analyses. We used these two grid sizes to examine landscape features at different scales and to make use of available satellite datasets.

We defined the primary breeding period as extending from 15 May to 1 July on the basis of our preliminary search data and reported nest timing for Surf Scoters (Savard and Lamothe 1991, Savard et al. 1998). Although nests were not confirmed for the majority of the birds, we followed a similar approach to Ely et al. (2006, 2007) to identify where repeated locations in a small area indicated likely breeding activity. Surf Scoters are single-brooded and have an estimated incubation period of 28–30 days (Savard et al. 1998), so we defined the settling date (SETD) for a bird as the first day that it arrived to a nesting area (typically <20 km<sup>2</sup>) where an individual was located for ≥25 days. Since Surf Scoters have one of the shortest seasonal pair bonds among waterfowl and males leave females within three weeks after arrival on breeding lakes (Savard et al. 1998), we only analyzed data from females. We tested SETD differences among birds from different wintering areas with analysis of variance and presented 95% confidence intervals.





$$\bar{d} = (d1 + d2 + d3 + d4 + d5 + d6)/6$$

$$C_1 = f(SF1) = 1/(d2 + \bar{d})$$

$$C_2 = f(SF2) = 1/(d2 + \bar{d})$$

$$C_3 = f(PS1) = 1/(d4 + \bar{d})$$

$$C_4 = f(PS2) = 0/(d3 + \bar{d})$$

$$C = \sum_{i=1}^4 C_i$$

Figure 4.2. Depiction of method used to calculate a nearest-neighbor cluster statistic  $C$  to examine differences in breeding locations for Surf Scoter areas wintering at four areas along the Pacific coast. Calculations were conducted for all pairs of locations, and statistical significance was determined with Monte Carlo simulations for 10,000 iterations under a null hypothesis of random mixing.

### Nearest-Neighbor Analysis

We adapted the two-cluster, nearest-neighbor approach of Schilling (1986) and applied to biological problems by Rosing et al. (1998) along with the scale-independent approach and weighting method of Day et al. (1989; see also Cuzick and Edwards, 1990) to develop our analysis. The null hypothesis was that the locations of marked Surf Scoters from different wintering areas were thoroughly mixed and distributed randomly, while our alternative hypothesis was that they were found in non-random clusters. For each scoter,  $i$ , we determined the distance,  $d_i$ , to the nearest scoter from any wintering area, and calculated a cluster statistic function,  $C_i = \delta_i/(d_i + \bar{d})$ , where  $\delta_i$  is an indicator function of whether the nearest scoter is of the same wintering area as scoter  $i$ , and  $\bar{d}$  is the average distance between all pairs of locations, independent of wintering area affiliation. The nearest neighbor cluster statistic  $C$  was set equal to the sum of all  $C_{-i}$  (Fig. 4.2).

We determined statistical significance with simulation tests by reassigning the wintering areas randomly to the configuration of locations while preserving the original sample sizes and recalculating  $C$ . We conducted a Monte Carlo simulation with 10,000 iterations to generate the distribution of  $C$  under the null hypothesis of random mixing. After determining the overall result among the four wintering areas, we repeated the Monte Carlo simulation of 10,000 iterations for each pair of wintering areas to examine spatial separation.

### Environmental Data

Boreal forest habitats have been characterized at different scales from general classification systems (Rempel et al. 1997), linking structure (environmental and biotic variables) and function (waterfowl use and productivity) to ground surveys relating wetland features (e.g., depth, area, perimeter, vegetation, amphipods) to brood-rearing use (Fast et al. 2004). We used remote-sensing data sets and characterized landscape features at a scale appropriate to describe a scoter's nesting area, determined from satellite telemetry locations with a rough accuracy of about 1 km. The landscape features are defined below and included: snow-free date, snow-free date difference, latitude, distance to treeline, distance to snowline on settling date, elevation, elevation gradient, number of lakes, water cover, ground cover, and tree cover. Elevation gradient and cover classes were estimated at two grid scales ( $2 \times 2$  km,  $4 \times 4$  km) similar to the scale of the satellite locations (1 km) to reduce potential cross-scale correlations (Battin and Lawler 2006). We used Hawth's Tools (Beyer 2004) to generate a set of random points, equal in number to the nesting birds found in a particular year (2003–2006), and to compare general NBF landscape features with the scoter nesting areas in an unconstrained design (Battin and Lawler 2006). Habitats unsuitable for nesting, such as mountain ranges devoid of trees, and very large lakes (i.e., Great Bear, Great Slave, Athabasca) were excluded from the analysis.

We estimated the snow-free date (SFDA), or the Julian Date when an area became snow-free, from the Interactive Multisensor Snow and Ice Mapping System (IMS), Daily Northern Hemisphere Snow and Ice Analysis coverage (NOAA/NESDIS/OSDPD/SSD 2006). A grid file was obtained for each day between 15 May and 1 July from 2003 to 2006 that was coded as 0 = no data, 1 = open water, 2 = snow-free land, 3 = ocean or lake ice, or 4 = snow-covered land. The files were converted to raster format and displayed in ArcMap. Although the coverage was updated daily, the IMS is manually derived based on visual imagery, and persistent cloud cover may have resulted in large changes in snow cover between some updates. Snow cover varied greatly among years, so we used the same number of random points as nesting birds in each year to make the data set balanced. Thus, there were 7 random points for 2003, 3 for 2004, 26 for 2005, and 17 for 2006, and a random date was selected from the breeding period (15 May to 1 July) and assigned to that point.

We estimated snow-free date difference (SFDD) as the number of days between the settling date for a scoter and the snowmelt date at its nesting area. Negative values indicated by how many days the settling date preceded the snowmelt, zero indicated that the bird arrived on the date the area became snow-free, and positive values indicated the number of days after snowmelt that the bird arrived.

Distance to snowline (DSNO) was estimated as minimum distance (km) from the mean location of a nesting bird to the snowline (the boundary line coverage rather than individual pixels estimated from the IMS) on that bird's settling date as the snowline retreated to the northeast.

We estimated the distance to treeline (DTRE) as the minimum distance from the nesting location to the nearest edge of the treeline in Canada (treeline coverage, Ducks Unlimited Canada). The coverage did not extend into eastern Alaska, so here we estimated the treeline edge by determining the percent of tree cover (see vegetation cover below) below 5%.

Latitude (LATD) was recorded as decimal degrees for random points and the estimated center point of the nesting areas.

Elevation (ELEV; meters) and elevation gradient (ELG2, ELG4) at  $2 \times 2$  km and  $4 \times 4$  km scales were estimated from topographic coverages

converted from program Mapsource (Garmin International, Inc., Topo Canada, v. 2, Olathe, KS). Topographic maps were obtained for each location and registered with three control points. Program FastStone Capture was used to save these maps as image files, which were then reprojected for analyses to NAD 83, Zone 10 (ArcCatalog). For elevation gradient, we calculated the difference between the minimum and maximum elevation (m) and divided it by the horizontal distance (km) across a grid square at a particular scale.

The number of lakes (NLK2, NLK4) within  $2 \times 2$  km or  $4 \times 4$  km grids was estimated from the topographic coverages. A lake was included if any part of it was found within a particular grid. Water cover (WCV2, WCV4) was determined at  $2 \times 2$  km and  $4 \times 4$  km scales from the topographic coverages. Water cover estimated the total percentage of a grid covered by water, unlike the NLK2 and NLK4 variables that determined whether Surf Scoters were found in areas with a few large lakes or a small number of lakes. For each bird and random point, we used the screen capture (FastStone Capture) and grayscale conversion (Scion Image) programs. The spatial scale of the images was standardized (Tool "Set Scale") and pixels with water were selected (Tool "Density Slice") by their grayscale values to estimate the extent of lakes and streams (Tool "Measure").

Vegetation cover was determined in  $2 \times 2$  km and  $4 \times 4$  km grids from satellite data obtained by the Moderate-resolution Imaging Spectroradiometer (MODIS) instrument and the vegetation continuous field coverage (Hansen et al. 2001). The MODIS satellite data were projected in WGS 84 with a resolution of 500 m, and we used the vegetation continuous field data (Hansen et al. 2001) to obtain estimates of vegetation cover from 31 October 2000 to 9 December 2001 (Global Land Cover Facility, College Park, MD, <http://www.landcover.org>). We selected grid cells with the Thematic Raster Summary Tool (Beyer 2004) to determine the percent coverage of each cover type. Each pixel included a value for percent ground cover (GCV2, GCV4), tree cover (TCV2, TCV4), and bare ground (BAR2, BAR4). The cover types comprised a composition that added to 1; therefore, we reported the means but excluded percent cover of bare ground (BAR2, BAR4) in analyses since it was dependent on the other variables.

TABLE 4.1  
Landscape features (mean  $\pm$  SE) for Surf Scoters ( $n = 53$ ) nesting in the northern boreal forest (NBF) from different wintering areas

Detailed explanation of variables is provided in Methods.

Variable	San Quintin Bay, Baja California Norte, Mexico	San Francisco Bay, California, USA	Puget Sound, Washington, USA	Strait of Georgia, British Columbia, Canada
Snow-free date (Julian Date)	146.0 $\pm$ 2.0	145.5 $\pm$ 2.5	148 $\pm$ 2.7	148.5 $\pm$ 3.8
Snow-free date difference	14.3 $\pm$ 3.3	4.2 $\pm$ 2.3	2.2 $\pm$ 2.4	2.8 $\pm$ 2.3
Latitude in decimal degrees	66.1 $\pm$ 1.9	64.0 $\pm$ 0.6	63.3 $\pm$ 0.7	64.8 $\pm$ 1.5
Distance to treeline	116 $\pm$ 29	174 $\pm$ 20	224 $\pm$ 35	169 $\pm$ 28
Distance to snowline	56 $\pm$ 33	77 $\pm$ 16	75 $\pm$ 14	34 $\pm$ 10
Elevation	246 $\pm$ 25	312 $\pm$ 26	349 $\pm$ 26	329 $\pm$ 53
Variables at two grid scales ( $2 \times 2$ and $4 \times 4$ km)				
Elevation gradient ( $2 \times 2$ km)	7.1 $\pm$ 3.5	5.0 $\pm$ 1.2	6.9 $\pm$ 1.6	7.1 $\pm$ 4.1
Elevation gradient ( $4 \times 4$ km)	4.1 $\pm$ 2.1	7.8 $\pm$ 2.1	5.6 $\pm$ 1.3	5.8 $\pm$ 2.2
Number of lakes ( $2 \times 2$ km)	6.7 $\pm$ 2.3	6.7 $\pm$ 0.9	4.0 $\pm$ 0.5	4.8 $\pm$ 0.8
Number of lakes ( $4 \times 4$ km)	23.3 $\pm$ 2.6	24.4 $\pm$ 8.3	14.0 $\pm$ 3.6	13.0 $\pm$ 2.8
Water cover ( $2 \times 2$ km)	0.283 $\pm$ 0.145	0.165 $\pm$ 0.020	0.190 $\pm$ 0.037	0.133 $\pm$ 0.034
Water cover ( $4 \times 4$ km)	0.180 $\pm$ 0.075	0.150 $\pm$ 0.014	0.147 $\pm$ 0.020	0.163 $\pm$ 0.040
Bare ground ( $2 \times 2$ km)	0.050 $\pm$ 0.010	0.082 $\pm$ 0.011	0.066 $\pm$ 0.012	0.113 $\pm$ 0.029
Bare ground ( $4 \times 4$ km)	0.073 $\pm$ 0.015	0.090 $\pm$ 0.009	0.065 $\pm$ 0.011	0.095 $\pm$ 0.015
Ground cover ( $2 \times 2$ km)	0.520 $\pm$ 0.122	0.572 $\pm$ 0.017	0.542 $\pm$ 0.031	0.628 $\pm$ 0.052
Ground cover ( $4 \times 4$ km)	0.597 $\pm$ 0.066	0.589 $\pm$ 0.016	0.567 $\pm$ 0.017	0.603 $\pm$ 0.031
Tree cover ( $2 \times 2$ km)	0.147 $\pm$ 0.015	0.179 $\pm$ 0.015	0.203 $\pm$ 0.023	0.133 $\pm$ 0.040
Tree cover ( $4 \times 4$ km)	0.153 $\pm$ 0.015	0.172 $\pm$ 0.014	0.222 $\pm$ 0.023	0.143 $\pm$ 0.027

#### Nesting Area Selection

We used logistic regression to model the selection of nesting areas on the basis of characteristics associated with the timing and location of breeding (Table 4.1; Manly et al. 2002). We applied second-order Akaike's Information Criterion ( $AIC_c$ ; Burnham and Anderson 2002) to select the best model from a series of candidate logistic regression models comparing characteristics of scoter nesting areas with randomly selected points. Small sample sizes of birds in some wintering areas limited our ability to test differences among years; therefore, we pooled the samples across years. AIC values and Akaike weights were calculated for candidate models under logistic

regression (Burnham and Anderson 2002, SAS Institute 2004).

We used a second-order AIC:  $AIC_c = -2(\log\text{-likelihood}) + 2KN/(N - K - 1)$ , where  $K$  is the number of fitted parameters including variance and  $N$  is the sample size (Anderson et al. 2000; Burnham and Anderson 2002). We considered the model with the smallest  $AIC_c$  to be the most parsimonious (Anderson et al. 2000; Burnham and Anderson 2002). We calculated the  $AIC_c$  differences between the best model and the other candidate models ( $\Delta AIC_{ci} = AIC_{ci} - \text{minimum } AIC_c$ ). Akaike weights ( $w_i = \exp[-\Delta AIC_{ci}/2]/\sum \exp[-\Delta AIC_{ci}/2]$ ) were calculated to assess the evidence that the selected model was the best Kullback–Leibler model (Anderson et al. 2000; Burnham and Anderson 2008).

The number of possible models built from combinations of 17 variables ( $n = 2^{17} - 1$ ) exceeded that which could be reasonably examined to determine their relative ranking. However, estimating  $AIC_c$  for a smaller subset of the possible variable combinations could exclude the best models (Steidl 2006), and it was not clear that grouping certain variables would be appropriate. Therefore, we conducted model selection by AIC in multiple stages. Our initial set of models was selected *a priori* to any analyses and included single-effect models and the full-term model containing all 17 variables. We hypothesized that any effect of latitude could differ among Surf Scoters from different wintering populations (WPOP), so we included WPOP and LATD\*WPOP terms in the full-term model. If the full-term model fit best, then this indicated a better model existed based on combinations of variables. We then used a stepwise approach as recommended by Steidl (2006) to find the models with combinations of variables that produced the lowest  $AIC_c$  value.

We conducted both a backward stepwise analysis, removing a single variable at a time from the full-term model, and a forward stepwise analysis, entering a single variable at a time to the null (intercept-only) model. We used  $AIC_c$  as a criterion for each forward or backward step by selecting the variable in which its addition or removal contributed to the greatest reduction in the  $AIC_c$ , until no single addition or removal would further reduce the  $AIC_c$ . Since different models can result from forward and backward stepwise selection, we used  $AIC_c$  to select the better of the two models. We included any model with a  $\Delta AIC_c$  within 2 units of the best model and reported the evidence ratio to compare the relative likelihood of probability between two models (Burnham and Anderson 2002). We calculated odds ratios (OR) for variables in the best model to determine if locations with higher values of these variables were more ( $OR > 1$ ) or less likely ( $OR < 1$ ) to become nesting area locations.

We then applied a classification and regression tree (CART) to confirm the direction and significance of effects in the best model (Stephens et al. 2005) and to examine cross-scale correlation (Battin and Lawler 2006). CART models are in the form of nonparametric, dichotomous keys (Brieman et al. 1984, De'ath and Fabricus 2000, Maisonneuve et al. 2006). CART algorithms partitioned the locations into subsets by recursively

splitting explanatory variables into high and low categories which significantly contribute to the prediction of Surf Scoter nesting areas. The recursive partitioning of the data into subcategories within categories enabled our analysis to naturally explore and identify interaction effects, which would have been cumbersome with the logistic regression approach. CART was estimated from the "modeltools" and "party" packages for R software at the 0.10 significance criterion (R Development Core Team 2008; Hothorn et al. 2006, 2008).

## RESULTS

### Total Marked

From 2003 to 2006, 415 Surf Scoters were captured and radio-marked on the Pacific coast (Table 4.2) during the nonbreeding season, including 313 VHF-marked and 102 PTT-marked individuals. When we censored the males, the total sample was reduced by 66 individuals (16%). Of the remaining 349 marked Surf Scoters, only 55 females were found at inland locations where they stayed long enough to confirm their nesting locations. Eight of the 55 birds were located in two consecutive years (2005–2006), but we only used the first year in our analyses, so all samples were independent and based on different individuals. Finally, we located nests for three Surf Scoters, one PTT-marked bird and two VHF-marked birds, but we lacked repeated locations for the VHF-marked birds to estimate environmental conditions when they settled at nesting areas. Thus, we used a sample size of 53 Surf Scoters for our analyses.

### Settling Date

We used a conservative approach to estimate SETD for nesting Surf Scoters by (1) restricting our analyses to Argos location quality classes 1–3 and (2) limiting the birds to those that were repeatedly located at a site for at least 25 days. Our analysis indicated the mean SETD ( $\pm$ SE) was Julian Date  $151 \pm 0.9$  d, or 31 May. Mean SETD varied ( $F_{3,52} = 2.70$ ,  $P = 0.056$ ) by wintering area, ranging from PS:  $149.7 \pm 1.1$  ( $n = 21$ ); SF:  $149.8 \pm 1.4$  ( $n = 25$ ); SG:  $151.3 \pm 3.2$  ( $n = 4$ ); and SQ:  $160.3 \pm 4.7$  ( $n = 3$ ). The 95% confidence intervals (SQ: 153.2–167.4; SG: 145.1–157.4; SF: 147.3–152.2; and PS: 149.7–152.3) indicated that SETD was later for the southernmost wintering area (SQ), but was overlapping for the other wintering areas.



TABLE 4.2  
*Summary of Surf Scoters marked with very high frequency (VHF) or platform transmitter terminal (PTT) satellite transmitters in 2003–2006 from four different wintering areas*

Numbers in parentheses denote the total number of birds used for breeding ground analyses (see Methods).

Year	San Quintin Bay, Baja California Norte, Mexico		San Francisco Bay, California, USA <sup>a</sup>		Puget Sound, Washington, USA		Strait of Georgia, British Columbia, Canada	
	VHF	PTT	VHF	PTT	VHF	PTT	VHF	PTT
2003	0	0	33	8 (7)	0	0	0	0
2004	0	0	0	0	25	14 (3)	0	0
2005	14	5 (1)	87	11 (9)	35	22 (12)	77	8 (4)
2006	17	5 (2)	40	12 (9)	30	17 (6)	0	0
Total <sup>b</sup>	31	10 (3)	127	31 (25)	78	53 (21)	77	8 (4)

<sup>a</sup> The nests of three San Francisco Bay birds (2 VHF, 1 PTT) were located in ground searches, but the two VHF birds were not included in analyses because their settling dates were unknown.

<sup>b</sup> Eight birds marked in 2005 and also located in 2006 are not included twice.

#### Breeding Distribution

Surf Scoters from Pacific coast wintering areas used a relatively narrow, core breeding area from Lake Athabasca northwest to the Anderson River near the Arctic Ocean, with the distribution centered on the Great Slave and Great Bear Lakes in the Northwest Territories (Fig. 4.1). Surf Scoters

were distributed between 57.7°N and 69.0°N latitude, and 147.2°W and 96.5°W longitude. Nesting locations for eight birds from two different wintering areas (SF = 5, PS = 3) were located in two consecutive years and showed remarkable nesting area fidelity (Table 4.3; Fig. 4.3). The center of their nesting areas was located within 1.3 km ± 0.2 km of each other in subsequent years, but

TABLE 4.3  
*Remarkable nesting area fidelity of Pacific coast Surf Scoters found in the northern boreal forest in two consecutive years*

Wintering area, settling date (Julian Date), longitude and latitude (decimal degrees), and mean distance between nesting areas (km) are reported for each individual.

Bird <sup>a</sup>	Wintering Area	Year 1			Year 2			Distance (km)
		Settling Date	Longitude (°W)	Latitude (°N)	Settling Date	Longitude (°W)	Latitude (°N)	
40843	PS	146	123.161	64.169	167	123.162	64.165	0.52
43888	PS	145	119.623	62.360	145	119.622	62.355	0.63
43892	PS	146	116.584	64.184	158	116.596	64.179	0.71
53978	PS	149	106.645	60.021	152	106.620	60.024	1.47
53980	PS	146	111.058	60.781	144	111.116	60.778	3.17
55912	SF	159	109.149	60.521	143	109.154	60.521	0.33
55914	SF	144	147.198	67.572	154	147.201	67.574	0.34
55919	SF	158	105.202	60.899	149	105.153	60.888	2.94
Mean	—	149	—	—	152	—	—	1.26

<sup>a</sup> Located in 2005 and 2006, except for 40843 and 43892, located in 2006 and 2007.



Figure 4.3. Remarkable breeding site philopatry exhibited by Surf Scoters located at the same nesting areas in two consecutive years. The center of the home range (circles) and 95% fixed kernel home ranges (lines) are depicted for 2005 (closed circle or line) and 2006 (open circle or line). Individuals shown are from Puget Sound (40802, 40843, 43888, 43982, 53978, 53980) and San Francisco Bay (55912, 55914) wintering areas, but sample sizes were only adequate to create home ranges for three individuals (43888, 43982, 55912) in 2006.

TABLE 4.4

*Nearest-neighbor analysis for Surf Scoters wintering at four areas on the Pacific coast*

Table values include sample size ( $n$ ), the generated C-statistic, expectation of C, standard deviation of C, and probability on the basis of 10,000 Monte Carlo iterations.

Comparison	$n$	$C$	$E(C)$	$SD(C)$	Prob.
Overall	53	0.031	0.025	0.0052	0.1496
San Quintin Bay, Strait of Georgia	7	0.003	0.004	0.0022	0.6612
San Quintin Bay, San Francisco Bay	28	0.027	0.027	0.0020	0.3434
San Quintin Bay, Strait of Georgia	24	0.019	0.023	0.0019	0.9633
Strait of Georgia, San Francisco Bay	29	0.029	0.026	0.0023	0.1714
Strait of Georgia, Puget Sound	25	0.026	0.022	0.0024	0.0764
San Francisco Bay, Puget Sound	46	0.032	0.028	0.0052	0.1873

since we were unable to locate the exact nest location, we could not confirm if they used the same nest site.

#### Nearest-Neighbor Analysis

We were unable to reject the overall null hypothesis that breeding Surf Scoters from different Pacific coast wintering areas were thoroughly mixed and distributed randomly (Table 4.4). Surprisingly, the strongest evidence ( $P = 0.0764$ ) for clustering of Surf Scoters on the breeding grounds was among those individuals from PS and SG, separated by only 200 km in the winter. We were unable to reject random mixing in pairwise comparisons of the other wintering areas.

#### Nesting Area Selection

We were able to locate three nests of Surf Scoters by landing and searching the vicinity of locations in 2005–2006 (Fig. 4.4A–D). In general, nesting site vegetation was characterized by sparse black spruce (*Picea mariana*) trees (>4 m in height, 90% cover above the nest) and ground cover in lakeshore bogs comprised primarily of Labrador tea (*Ledum groenlandicum*), cloudberry (*Rubus chamaemorus*), mountain cranberry (*Vaccinium vitis-idaea*), and lichen. Two of the nesting sites were found in granitic or metamorphic rock outcroppings with sparse (0–5%) soil cover. The nests were found near

oligotrophic shallow lakes, but not where other waterfowl were observed.

Comparison among models of nesting area variables indicated that the backward selection model with ten variables most closely fit the data (Akaike weight = 81%; Table 4.5). The forward stepwise procedure resulted in an eight-variable model with a much poorer fit to the data ( $\Delta AIC_c = 2.9$ , Akaike weight = 19%). In the forward selection model, DSNO entered first, followed by ELG2 and ELG4, with strong evidence in favor of entering versus not entering each variable ( $\Delta AIC_c > 5.9$ ; evidence ratio > 19). The variables NLK4, NLK2, and LATD entered next under weaker evidence ( $\Delta AIC_c < 0.76$ ; evidence ratio < 1.5), followed by DTRE ( $\Delta AIC_c = 4.8$ ; evidence ratio = 11.3), and finally TCV4 ( $\Delta AIC_c = 0.88$ ; evidence ratio = 1.6). Both the backward and forward selection models fit the data better than the full-term model or the null model ( $\Delta AIC_c > 26$ ; evidence ratio = 100,000) and contained seven variables in common: DSNO, ELG2, ELG4, DTRE, LATD, NLK2, and NLK4. Odds ratios for these variables based on model averaging suggested that nesting Surf Scoters tended to settle nearer to snowline (OR = 0.983; 95% CI = 0.971–0.995; Fig. 4.5), in areas with less elevation gradient at  $2 \times 2$  km (OR = 0.912; 95% CI = 0.857–0.971) and  $4 \times 4$  km (OR = 0.960; 95% CI = 0.909–1.013) scales, in areas with fewer lakes at  $2 \times 2$  km (OR = 0.784; 95% CI = 0.639–0.964) but more lakes at  $4 \times 4$  km (OR = 1.246; 95% CI = 1.057–1.470), farther from treeline (OR = 1.013; 95%



Figure 4.4. Surf Scoters nesting within the northern boreal forest: (A) aerial view of nesting site, (B) ground view of nesting site, (C) female scoter on a nest, and (D) clutch of Surf Scoters eggs (11 June). USGS photo credit: E. Palm.



TABLE 4.5

Ranking of candidate Akaike Information Criterion (AIC) models  
to describe nesting areas of Surf Scoters breeding in the northern boreal forest

Backward and forward stepwise methods were used to select the two best models from the numerous combinations of the 17 variables that are presented with the full-term model (all variables) and null model (intercept only).

Model	N	K	-2 Log-likelihood	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Akaike Weight (%)
LATD, DTRE, DSNO, ELEV, ELG2, ELG4, NLK2, NLK4, WCV2, GCV2 <sup>a</sup>	106	11	54.1	78.9	0.0	81
LATD, DTRE, DSNO, ELG2, ELG4, NLK2, NLK4, TCV4 <sup>b</sup>	106	9	61.9	81.8	2.9	19
SFDA, SFDD, LATD, WPOP, LATD*WPOP, DTRE, DSNO, ELEV, ELG2, ELG4, NLK2, NLK4, WCV2, WCV4, GCV2, GCV4, TCV2, TCV4 <sup>c</sup>	106	23	46.0	105.5	26.6	0
Null Model (intercept only) <sup>d</sup>	106	0	146.9	146.9	68.1	0

NOTE: Variables include snow-free date (Julian Date: SFDA); snow-free date difference (SFDD); latitude in decimal degrees (LATD); wintering population (WPOP); distance to treeline (m; DTRE); distance to snowline (m; DSNO); elevation (m; ELEV); and variables at two grid scales (2 × 2 km and 4 × 4 km), including elevation gradient (ELG2, ELG4), number of lakes (NLK2, NLK4), water cover (WCV2, WCV4), ground cover (GCV2, GCV4), and tree cover (TCV2, TCV4). Detailed explanation of variables is provided in Methods.

<sup>a</sup> Backward selection model includes intercept and 10 variables.

<sup>b</sup> Forward selection model includes intercept and 8 variables.

<sup>c</sup> Full model includes intercept, 17 variables, and LATD\*WPOP interaction.

<sup>d</sup> In null model, *k* is zero since the intercept for the null model is known with equal sample sizes of nesting areas and random locations.

CI = 1.003–1.023), and at higher latitudes (OR = 1.500; 95% CI = 1.087–2.072).

The CART analysis (Fig. 4.6) split variables in a categorical tree that included elements from both the forward and backward selection models, consistent with the effects of DSNO, NLK4, ELG4, and ELG2 determined by the logistic regression. DSNO was the first significant predictor, with nesting areas comprising 2.9% of locations (1/34) at >218 km from snowline compared with 72.2% (52/72) at ≤218 km (left branch). Two variables at the larger (4 × 4 km) scale, NLK4 and ELG4, were the next most important predictors depending on distance to snowline. For locations >218 km from snowline, nesting sites comprised 9.1% (1/11) of locations with >7 lakes, compared with 0% (0/23) where there were ≤7 lakes. For locations ≤218 km from snowline, nesting locations comprised 33.3% (3/9) when elevation gradient was >14.1 m/km at the larger scale, compared with 77.8% (49/63) when ≤14.1 m/km (middle branch). For these latter locations, nesting areas comprised 89.7% (26/29) of locations at the smaller scale (2 × 2 km) where elevation gradient was ≤3.5 m/km, compared with 67.6% (23/34)

of locations where elevation gradient was higher. The CART analysis detected positive and negative effects associated with number of lakes at the small scale, depending on the elevation gradient. For low elevation gradients, nesting locations comprised 95.0% of locations with ≤6 lakes (19/20), compared to 77.8% where there were more lakes (7/9). In contrast, for higher elevation gradients, nesting locations comprised only 37.5% of locations with ≤6 lakes (6/16), compared to 94.4% where there were more lakes (17/18).

## DISCUSSION

We integrated data sets from four different wintering areas along the Pacific coast to delineate the western breeding range for our sample of radio-marked Surf Scoters. Rather than finding wide temporal and spatial variation that might be expected for a species with a large breeding range in an ecosystem characterized by extreme variation (Chapin et al. 2006), we found that Surf Scoters settled in a relatively narrow arc of habitat parallel to the receding snowline. Also, the timing of their breeding was synchronous, as most



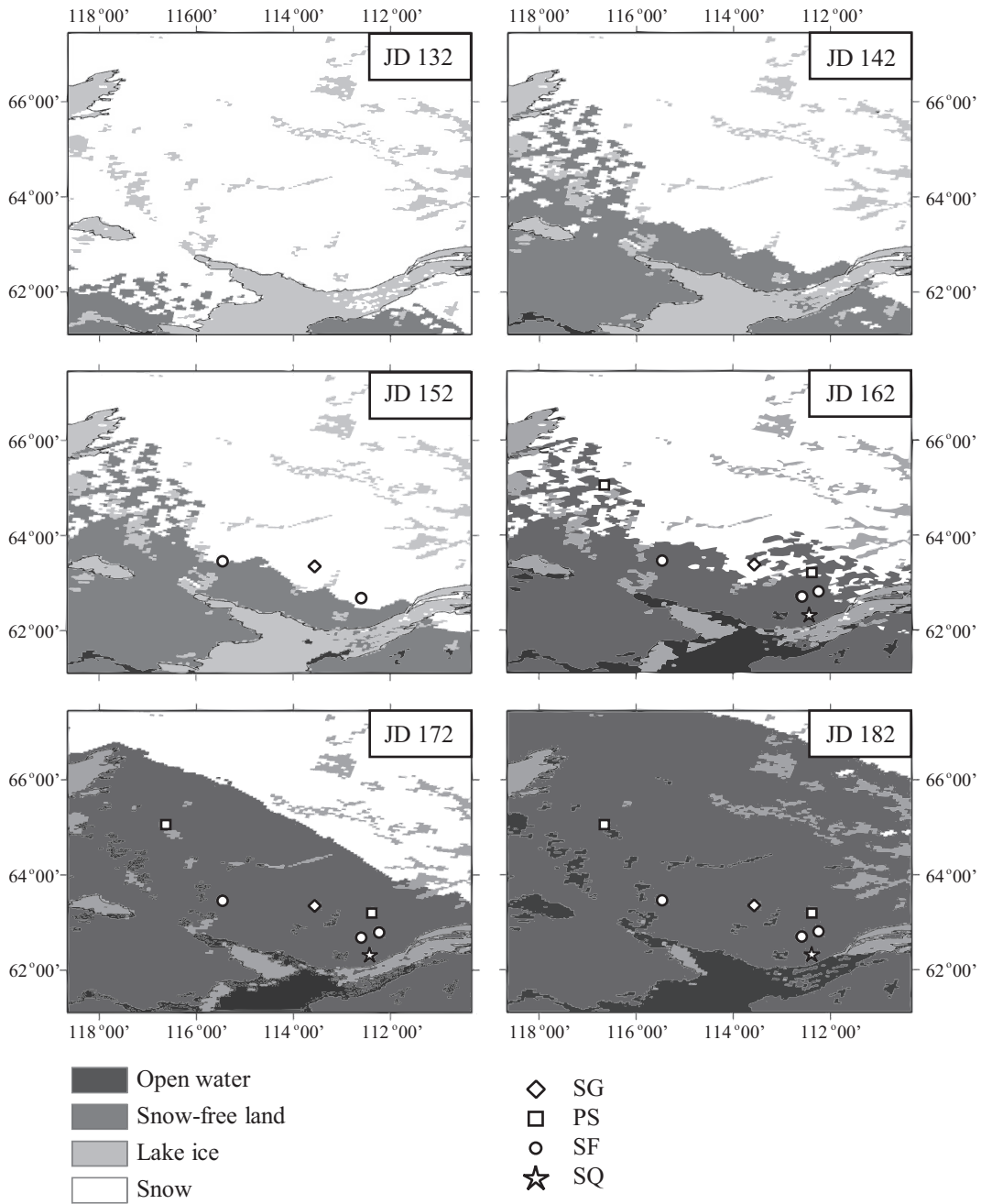


Figure 4.5. Seasonal variation (10-day intervals) in availability of habitats for Pacific coast Surf Scoters breeding in the northern boreal forest, where Julian Date (JD) 152 = 1 June. Snow-melt progression was determined with daily satellite images ( $4 \times 4$  km pixels) from the Interactive Multisensor Snow and Ice Mapping System (IMS), Daily Northern Hemisphere Snow and Ice Analysis coverage (NOAA/NESDIS/OSDPD/SSD 2006).

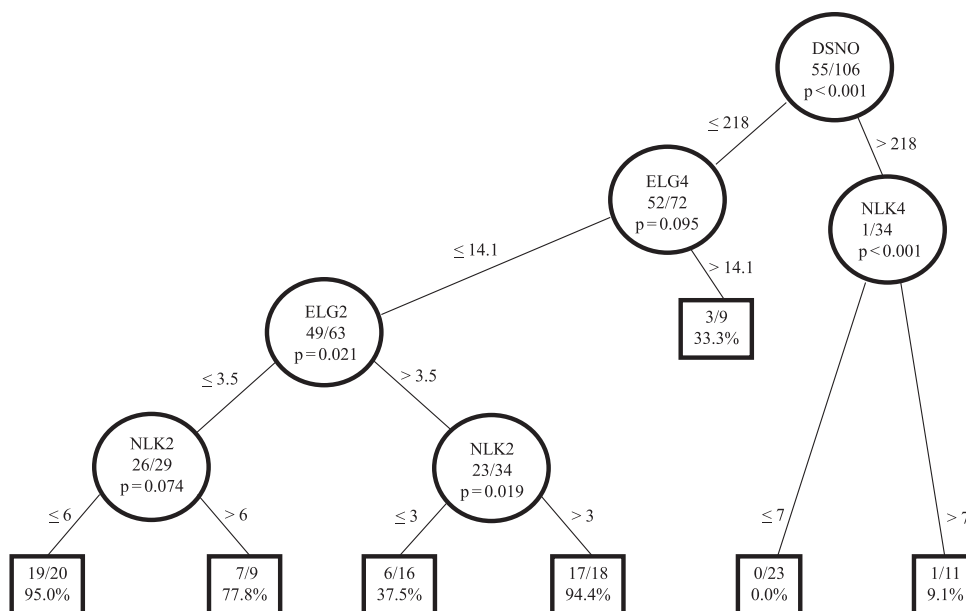


Figure 4.6. Classification and regression tree (CART) for Pacific coast Surf Scoters breeding in the northern boreal forest. The explanatory variable being split, the number of Surf Scoter breeding locations in the numerator and number of total locations (nesting areas and random locations) in the denominator, and the p-value associated with the split are included in each circle. Splitting values are indicated along the branches, and boxes indicate terminal node percentages of total locations comprised of Surf Scoter breeding locations. Splitting variables include distance to snowline (DSNO), elevation gradient (m/km) at  $4 \times 4$  km (ELG4) and  $2 \times 2$  km (ELG2), and number of lakes at  $4 \times 4$  km (NLK4) and  $2 \times 2$  km (NLK2).

individuals settled at nesting areas within a day of 30 May. Birds from different wintering areas were intermixed on the breeding grounds. A subsample of eight marked birds located in consecutive years showed strong nesting area fidelity.

#### Breeding Synchrony and Breeding Strategies

We found remarkable breeding synchrony for most birds regardless of their wintering origin and differences in distances from the breeding grounds. Birds wintering in Mexico were the only ones that arrived slightly later, although their sample size was small. Surf Scoters began arriving to their NBF breeding grounds around 24 May (JD =  $144 \pm 0.7$ ; De La Cruz et al. 2009) and flew to nesting areas along the northeastern edge of their breeding range. They settled at nesting areas after only five days during the ice and snow breakup period, when availability of open water and food resources would be uncertain. This short pre-breeding period was similar to Barnacle Geese (*Branta leucopsis*), which had a pre-breeding period of <7 days (Prop et al. 2003).

Although early-arriving migrants may be more likely to breed successfully (Cooke et al. 1995, LePage et al. 2000), timing of migration must fit a narrow time window to provide maximal reproductive success (Drent et al. 2003). Surf Scoters must depart from coastal staging areas on a schedule to optimize their breeding opportunities, but they seem to have few proximate clues that would help predict interior weather conditions more than 1,000 km away. Significant capital investment is likely required for Surf Scoters to reproduce successfully in light of the unpredictable pre-breeding resources and the short Arctic summer period (Klaassen et al. 2006). On a capital–income breeder continuum (Klaassen et al. 2006), Surf Scoters are expected to be on the capital breeder side since they have a short breeding period, unpredictable food resources, and high predation risk (Jonsson 1997). Schmutz et al. (2006) examined isotope ratios and found that marine food from coastal stopovers was used for incubation by Emperor Geese (*Chen canagica*), but eggs had mixed ratios from exogenous and endogenous sources. Similarly, White-winged Scoters were reported to rely

on exogenous resources for pre-laying and laying periods (Brown and Frederickson 1986).

In one of the few other studies to determine settling dates for waterfowl in the NBF, Ely et al. (2006) found earlier nest initiation (12 May) with less synchrony (8–16 May) for Tule Greater White-fronted Geese (*Anser albifrons elgasi*). However, this study was limited to VHF-marked individuals and defined nesting in upper Cook Inlet of central Alaska as those individuals located repeatedly for 1–2 weeks. Furthermore, Tule Greater White-fronted Geese may have less synchronous settling dates because they nest at lower latitudes, likely have more time to select nesting sites, and are larger, with lower risk of predation than Surf Scoters. Predation caused 76% of nest failures for another diving duck species that breeds in the NBF, the Lesser Scaup (*Aythya affinis*; Walker et al. 2005). The wide variation in annual recruitment rates seen in Lesser Scaup (Walker et al. 2005) is probably common for Surf Scoters, since their average annual nest success is very low (Savard et al. 1998).

In all likelihood, many more of the marked Surf Scoters were prospecting for nest sites early in the breeding season but their attempts to nest failed (S. W. De La Cruz, unpubl. data). Several VHF-marked females were located in the breeding area and appeared to be nesting, but subsequent trips to find their nests revealed that these birds had moved from their original positions. We suspect that their nests had been depredated, particularly since high nest depredation rates were noted by other researchers in the NWT (S. Slattery, Ducks Unlimited Canada, pers. comm.). In addition, small mammal populations were low and avian predators were markedly higher starting in 2005, when the majority of scoters were marked, than in previous years (S. Carrier, NWT Renewable Resources and Economic Development, pers. comm.). Waterfowl and their eggs may have provided an attractive alternative food source for predators (Ackerman 2002, Brook et al. 2005).

#### Wintering and Breeding Area Connectivity

Many species of migratory birds segregate by sex and age during the winter, often along latitudinal gradients (Ketterson and Nolan 1983), but few studies have linked breeding and wintering area subpopulations. Latitudinal variation of wintering Arctic nesting geese from different breeding grounds has been described (Ely and Takekawa 1996), and

variation in migration distances for Pacific Black Brant (*Branta bernicla nigricans*) migrating from wintering to breeding areas also has been documented (Schamber et al. 2007). Migration distance of Pacific Black Brant may be related to distribution of the eelgrass beds (*Zostera* spp.) that provide their primary food resource (Ward et al. 2005, Lindberg et al. 2007). Eelgrass beds also provide spawning habitat for Pacific herring (*Clupea pallasii*), and herring roe is a food resource consumed preferentially by Surf Scoters (Lewis et al. 2005).

We did not see a parallel relationship among latitudes at wintering and breeding areas where birds from more southerly areas were found at lower latitudes on the breeding grounds. We found that Surf Scoters from different wintering areas were randomly distributed on the breeding grounds. Surf Scoters from wintering areas were intermixed, although many PS birds migrated separately through the interior rather than following the coast (De La Cruz et al., 2009).

For the eight birds that were located nesting in consecutive years, we found philopatry and high nesting area fidelity. Female waterfowl show a high degree of nesting area fidelity, and the “local-knowledge” hypothesis suggests that females obtain an advantage in terms of food resources, distribution of conspecifics, and predator activity in an area (Rohwer 1992). For species such as sea ducks that form pairs in the winter, winter site fidelity may also be observed (Robertson and Cooke 1999). During our studies, few marked Surf Scoters moved among wintering areas during a single season, but one adult female marked in SF during 2005 flew to SQ during the winter of 2006. Complementary genetic analyses may be useful to further clarify the genetic structuring of these wintering populations.

#### Nesting Area Selection

Selection of breeding habitats by birds is considered to be hierarchical (Johnson 1980, Jones 2001), with different processes affecting different scales (Wiens 1989). We applied an unconstrained design that assumed selection varied at different scales (Battin and Lawler 2006) and focused our analyses at scales that we felt were appropriate for the accuracy of satellite-transmitter data. Compared with random locations in the NBF, both the logistic regression and CART analyses found consistent evidence that Surf Scoter nesting areas were located closer to the snowline and in areas with lower elevational

gradients and more lakes ( $4 \times 4$  km scale). Both analyses also detected effects associated with lakes at the smaller scale ( $2 \times 2$  km); however, the CART suggests this effect may interact with elevation gradient rather than stand alone as a main effect. Our logistic regression also suggests that Surf Scoters selected locations farther from the treeline and at higher latitudes. The CART did not confirm these additional effects; however, after partitioning the data with respect to the strongest predictors, there may have been too little data within any of the partitions for the CART to identify further effects.

Sea ducks are the most northerly distributed ducks (Goudie et al. 1994), and we hypothesized that snow conditions could be critical in determining nesting area. In fact, distance to snowline was the greatest single factor in the AIC score. The date when an area was snow free and the variation around that date were only ranked highly in backward selection, possibly because these variables were not completely independent and birds were selecting open habitats at finer scales. Because elevation was not selected and elevation gradient was highly ranked at both scales, Surf Scoters were likely selecting areas where topographic variation resulted in earlier openings in snow cover in some areas. Habitat selection may vary when available habitats vary temporally (Warnock and Takekawa 1995, Dailey et al. 2007), and we were able to account for this changing availability of nesting areas through use of daily ice and snow cover data.

Breeding propensity, or the likelihood that birds will find adequate habitat available to initiate a breeding attempt (Petrie et al. 2000), is probably highly variable for Surf Scoters because the spring thaw varies each year. It may be especially variable for those species that nest in unpredictable and highly heterogeneous environments such as the Arctic. For example, a large proportion of arctic nesting geese may fail to breed in years of late snow melt (Barry 1962, Prop and Devries 1993, Ganter and Boyd 2000). Delayed snow melt can prevent access to nesting sites and impair acquisition of nutrients for egg formation of Lesser Snow Geese (*Chen c. caerulescens*; Ganter and Cooke 1996). Breeding propensity in Greater Snow Geese (*C. c. atlantica*) varied from 0.17 to 1.00, and spring snow cover was a critical determinant (Reed et al. 2004). Most females (>80%) bred when snow cover was low, but few (<30%) bred when snow cover was extensive.

Our CART analysis suggested that nesting areas were found in areas where there were 3–6 lakes at the  $2 \times 2$  km scale. At lower elevation gradients ( $\leq 3.5$  m/km), similar proportions of nesting areas were found regardless of number of lakes, possibly because the area was more homogeneous, but at higher elevation gradients ( $> 3.5$  m/km), more nests were located when there were more lakes that could support food resources. Similarly, Perry et al. (2006) found that Surf Scoters from the Atlantic coast were located in areas with large wetlands (22 ha) associated with small rivers and when there were 22 lakes found within 1 km of the presumed breeding lake. Surf Scoters are reported to use lakes less than 10 ha in size that are shallow (Decarie et al. 1995), possibly to avoid competition with fish that consume invertebrates or to avoid larger fish that may consume young ducklings (Mallory et al. 1994). Unfortunately, we were unable to assess water depth from the satellite data to examine if shallow depths were selected.

A few other variables were highlighted by the AIC analysis. Nesting area selection was positively related to latitude, supporting our finding that Surf Scoters selected nesting areas in the northeast part of the breeding range. Surf Scoters migrated past many apparently suitable areas to the southwest of the snowline, but the reason why they avoid those areas is not clear. Perrin's hypothesis (Drent 2006) suggests that timing of nesting activities is a compromise between survival of the adult and food resource availability for the young. Nesting area selection may be driven by security and food availability for Surf Scoters, since this long-lived species seems to have low annual nest success (Newton 1989, Clutton-Brock 1998, Savard et al. 1998). Ducklings hatch nearly a month after breakup, and they may benefit from greater availability of macroinvertebrates (Oswood et al. 2006). Nest predators may be less abundant in areas farther north. White-winged Scoters (*Melanitta fusca*) do nest in areas farther south, but they are larger, which may deter some predators, and often use islands to avoid other predators (Traylor et al. 2004, Perry et al. 2006).

The AIC analysis also suggested that nesting areas were negatively related to treeline and positively related to tree cover. Treelines are sensitive to changes in climate, as well as being proxies for biotic changes (reviewed in Payette 2007). Surf Scoters did not settle near treeline, possibly because tree and ground cover was too sparse to

provide adequate cover against predators or severe weather events. Perry et al. (2006) also found that most Surf Scoters from Atlantic coast wintering areas bred in forested areas. Surf Scoters may select smaller areas with adequate cover rather than larger, contiguous forested blocks. Fire frequency is high in the NBF (Kasischke et al. 2006), and the availability of contiguous forest blocks may be highly variable.

#### Implications of Climate Change for Surf Scoters in the Boreal Forest

The synchrony of breeding and the relation of nesting locations to snowline suggest that reproductive timing may be constrained by resource conditions. If adults are nesting earlier to maximize their own food resources, it may be that their breeding productivity depends on resource availability for their ducklings. Climate change is most pronounced at high latitudes (Serreze et al. 2000), and global warming may result in drastic changes in the timing of invertebrate blooms in the boreal forest. At Delta Marsh, Manitoba, waterfowl had the highest proportion of earlier arrivals among migratory birds, and arrival date was correlated with temperature (Murphy-Klassen et al. 2005). Weather at stop-over areas and at the final destination influences timing of bird migration (Richardson 1978). Dates of ice break-up are good predictors because open water plays a primary role in migration of waterfowl (Murphy-Klassen et al. 2005).

The spring mismatch hypothesis (Visser et al. 1998, Drever and Clark 2007) suggests that global warming may result in earlier or protracted blooms of invertebrates, resulting in less food available for ducklings during critical periods of early growth. Haszard (2004) found Surf Scoters pairs and broods in wetlands with more abundant food, but their use of wetlands was not clearly related to wetland amphipods. However, wetlands used by Lesser Scaup in the same region were strongly related to abundance of amphipods (Fast et al. 2004). Surf Scoters are relatively unique in that many ducklings gather together in large creches and largely fend for themselves within a few days after leaving the nest (Savard et al. 1998). Thus, the availability of abundant invertebrate prey in brood-rearing areas may be critical for duckling survival.

Global warming has been cited as a conservation concern for bird species throughout the world

(McCarty 2001) and may have greatest impacts on the most northerly nesting species, such as sea ducks. Birds respond by expanding their range northward, advancing breeding dates, or varying their timing of breeding to match phenology of their prey (Ward 1992, Drever and Clark 2007). Individuals or populations that are not able to adjust to warming may suffer reduced productivity because of limitations in egg production, or because of conflicts in wintering ground or migration cues compared with breeding timing (Both and Visser 2001). Under the individual optimization hypothesis (Drent 2006), timing of breeding is controlled by environmental factors, but endogenous controls (Gwinner 1996) may limit the ability of Surf Scoters to adapt to climatic changes.

#### Conservation Threats

A better understanding of scoter breeding ecology will aid managers in making informed land use decisions as development pressure increases. For example, our results identify a much smaller area where effort could be focused to examine declining populations of Surf Scoters from the Pacific coast. The need for this information is underscored by the imminent oil, gas, and diamond mining development planned in the NWT (Government of the Northwest Territories; Industry, Tourism, and Investment, <http://www.iti.gov.nt.ca/index.html>). Loss of habitat from logging, mining, and hydroelectric power production has been suspected of affecting Surf Scoters from the Atlantic coast (Perry et al. 2006).

Sustainable harvest rates in sea ducks may be lower than in many other species (Goudie et al. 1994), since sea ducks tend to be K-selected (Eadie et al. 1988). Sea ducks have deferred sexual maturity, low annual recruitment to breeding age, variable rates of non-breeding by adults and high annual adult survival (Goudie et al. 1994). Infrequent Arctic ice events may cause mass mortality (Barry 1968) or affect body condition and fitness of birds (Goudie and Ankney 1986). Thus, subtle changes in the frequency of catastrophic events may greatly reduce population levels over time.

#### ACKNOWLEDGMENTS

This study was funded by the U.S. Geological Survey (USGS) Western Ecological Research Center under the Coastal Ecosystems and Land-Sea Interface



Program. Additional assistance was provided by the CALFED Ecosystem Restoration Program Mercury Project, the Dennis Raveling Chair at the University of California, and the Sea Duck Joint Venture and NASA Signals of Spring. T. Bowman (SDJV) encouraged us to integrate our data, and we acknowledge the support of D. Mulcahy, S. Iverson, K. Brodhead, P. Fontaine, E. Bohman, C. Eldermire, A. Keech, S. Duarte-Etchart, S. Duarte, E. Lok, D. Rizzolo, K. Sage, and M. Shepherd (SQ); D. Gaube, L. Terrazas, J. Anhalt, C. Kereki, J. Chastant, H. Goyert, J. Wasley, J. Seyfried, P. Gibbons, M. Nagendran, C. Scott, P. Tucker, C. Salido (SF); Tom Cyra, Joe Gaydos, Briggs Hall, Dyanna Lambourn, Don Kraege, Bryan Murphie, and Greg Schirato (PS); the Canadian Wildlife Service of Environment Canada and National Science and Engineering Research Council (NSERC) strategic grant STPGP246079-01, the Centre for Wildlife Ecology, Simon Fraser University, and field assistance of E. Anderson, B. Bartzen, T. Bowman, S. Coulter, R. Dickson, G. Grigg, S. Iverson, D. Lacroix, T. Lewis, R. Lis, and R. Zydelski, D. Mulcahy, and M. McAdie for radio implantation (SG). On the breeding grounds, we were grateful for the assistance of C. Babcock and A. Fowler (UC Davis), who led the initial surveys in 2003, and K. Farke and I. Woo (USGS), who assisted in 2005. Also, special thanks to R. King, FWS Migratory Bird Management (retired) for flight support, J. Hines (CWS, Yellowknife, NWT) for assistance with housing and information, D. Douglas (USGS Alaska Science Center) for advice on remote-sensing data sources, and E. Butterworth (Ducks Unlimited Canada) for the western boreal forest and treeline coverages. We thank M. Mueller, S. Iverson, M. Casazza, and T. Bowman for helpful comments on earlier drafts. This work was conducted following guidance from Animal Care and Use Committees and with permits from California Department of Fish and Game, Canadian Wildlife Service, Northwest Territories RWED, U.S. Fish and Wildlife Service, USGS Bird Banding Laboratory, and Washington Department of Fish and Wildlife. We also thank the numerous local NWT communities that provided helpful information and permitted access to remote areas. Use of trade names does not imply government endorsement.

#### LITERATURE CITED

- Ackerman, J. T. 2002. Of mice and mallards: positive indirect effects of coexisting prey on waterfowl nest success. *Oikos* 98:469–480.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- Barry, T. W. 1962. Effects of late seasons on Atlantic Brant reproduction. *Journal of Wildlife Management* 26:19–26.
- Barry, T. W. 1968. Observations on natural mortality and native use of eider ducks along the Beaufort Sea coast. *Canadian Field-Naturalist* 82:140–144.
- Battin, J., and J. J. Lawler. 2006. Cross-scale correlation and the design and analysis of avian habitat selection studies. *Condor* 108:59–70.
- Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. <<http://www.spatial ecology.com/htools>>.
- Both, C., and M. E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* 411:296–298.
- Brieman, L., J. H. Friedman, R. A. Olshen, and C. J. Stone. 1984. Classification and regression trees. Wadsworth and Brooks, Monterey, CA.
- Brook, R. W., D. C. Duncan, J. E. Hines, S. Carriere, and R. G. Clark. 2005. Effects of small mammal cycles on productivity of boreal ducks. *Wildlife Biology* 11:3–11.
- Brown, P. W., and L. H. Frederickson. 1986. Food-habits of breeding White-winged Scoters. *Canadian Journal of Zoology* 64:1652–1654.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer Science+Business Media, Inc., New York, NY.
- Carlton, J. T., J. K. Thompson, L. E. Schemel, and F. H. Nichols. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. I: Introduction and dispersal. *Marine Ecology Progress Series* 66:81–94.
- Chapin, F. S., III, J. Yarie, K. Van Cleve, and L. A. Viereck. 2006. The conceptual basis of LTER studies in the Alaskan boreal forest. Pp. 3–11 in F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (editors), *Alaska's changing boreal forest*. Oxford University Press, New York, NY.
- Clutton-Brock, T. H. 1988. Reproductive success. University of Chicago Press, Chicago, IL.
- Cohen, A. N., and J. T. Carlton. 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. Report to U.S. Fish and Wildlife Service and National Sea Grant College Program, Connecticut Sea Grant.
- Cooke, F., R. F. Rockwell, and D. B. Blank. 1995. The Snow Geese of La Perouse Bay: natural selection in the wild. Oxford University Press, Oxford, UK.
- Cuzick, J., and R. Edwards. 1990. Spatial clustering for inhomogeneous populations. *Journal of the Royal Statistical Society B*. 52:73–104.
- Dailey, M., A. I. Gitelman, F. L. Ramsey, and S. Starcevic. 2007. Habitat selection models to account for

- seasonal persistence in radio telemetry data. *Environmental and Ecological Statistics* 14:55–68.
- Day, R., J. H. Ware, D. Wartenberg, and M. Zelen. 1989. An investigation of a reported cancer cluster in Randolph, Massachusetts. *Journal of Clinical Epidemiology* 42:137–150.
- De La Cruz, S. E. W., J. Y. Takekawa, M. T. Wilson, D. R. Nysewander, J. R. Evenson, D. Esler, W. S. Boyd, and D. H. Ward. 2009. Spring migration routes and chronology of Surf Scoters (*Melanitta perspicillata*): a synthesis of Pacific coast studies. *Canadian Journal of Zoology* 87:1069–1086.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192.
- Decarie, R., F. Morneau, D. Lambert, S. Carriere, and J.-P. L. Savard. 1995. Habitat use of brood-rearing waterfowl in subarctic Quebec. *Arctic* 48:383–390.
- Devries, J. H., J. J. Citta, M. S. Lindberg, D. W. Howerter, and M. G. Anderson. 2003. Breeding-season survival of mallard females in the Prairie Pothole Region of Canada. *Journal of Wildlife Management* 67:551–563.
- Drent, R. 2006. The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. *Ardea* 94:305–322.
- Drent, R., C. Both, M. Green, J. Madsen, and T. Piersma. 2003. Pay-offs and penalties of competing migratory schedules. *Oikos* 103:274–292.
- Drever, M. C., and R. G. Clark. 2007. Spring temperature, clutch initiation date and duck nest success: a test of the mismatch hypothesis. *Journal of Animal Ecology* 76:139–148.
- Eadie, J. M., F. P. Kehoe, and T. D. Nudds. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: a review of hypotheses. *Canadian Journal of Zoology* 66:1709–1721.
- Ely, C. R., K. S. Bollinger, R. V. Densmore, T. C. Rothe, M. J. Petrula, J. Y. Takekawa, and D. L. Orthmeyer. 2007. Reproductive strategies of northern geese: why wait? *Auk* 124:594–605.
- Ely, C. R., K. S. Bollinger, J. W. Hupp, D. V. Derksen, J. Terenzi, J. Y. Takekawa, D. L. Orthmeyer, T. C. Rothe, M. J. Petrula, and D. R. Yparraguirre. 2006. Traversing a boreal forest landscape: summer movements of Tule Greater White-fronted Geese. *Waterbirds* 29:43–55.
- Ely, C. R., and J. Y. Takekawa. 1996. Geographic variation in migratory behavior of Greater White-fronted Geese (*Anser albifrons*). *Auk* 113:889–901.
- ESRI. 1996. ArcView GIS: using ArcView GIS. Environmental Systems Research Institute, Inc., Redlands, CA.
- Fast, P. L. F., R. G. Clark, R. W. Brook, and J. E. Hines. 2004. Patterns of wetland use by brood-rearing Lesser Scaup in northern boreal forest of Canada. *Waterbirds* 27:177–182.
- Ganter, B., and H. Boyd. 2000. A tropical volcano, high predation pressure and the breeding biology of arctic waterbirds: a circumpolar review of breeding failure in the summer of 1992. *Arctic* 53:289–305.
- Ganter, B., and F. Cooke. 1996. Pre-incubation feeding activities and energy budgets of Snow Geese: can food on the breeding grounds influence fecundity? *Oecologia* 106:153–165.
- Goudie, R. I., and C. D. Ankney. 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. *Ecology* 67:1475–1482.
- Goudie, R. I., A. V. Kondratyev, S. Brault, M. R. Petersen, B. Conant, and K. Vermeer. 1994. The status of sea ducks in the north Pacific Rim: toward their conservation and management. *Transactions of the 59th North American Wildlife and Natural Resources Conference* 59:27–49.
- Gwinner, E. 1996. Circannual clocks in avian reproduction and migration. *Ibis* 138:47–63.
- Hansen, M., R. DeFries, J. R. Townshend, M. Carroll, C. Dimiceli, and R. Sohlberg. 2001. Vegetation continuous fields MOD44B, 2001 percent tree cover. Collection 4. University of Maryland. College Park, MD.
- Haszard, S. 2004. Habitat use by White-winged Scoters (*Melanitta fusca*) and Surf Scoters (*Melanitta perspicillata*) in the Mackenzie Delta region, Northwest Territories. Master's thesis, University of Saskatchewan, Saskatoon, SK.
- Hodges, J. I., J. G. King, B. Conant, and H. A. Hanson. 1996. Aerial surveys of waterbirds in Alaska 1957–94: population trends and observer variability. Information and Technology Report 4. U.S. National Biological Service and U.S. Fish and Wildlife Service.
- Hothorn, T., K. Hornik, and A. Zeileis. 2006. Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics*. 15:651–674.
- Hothorn, T., F. Leisch, and A. Zeileis. 2008. Modeltools: tools and classes for statistical models. R package version 0.2-15.
- Iverson, S. A., W. S. Boyd, D. Esler, D. M. Mulcahy, and T. D. Bowman. 2006. Comparison of the effects and performance of four types of radiotransmitters for use with scoters. *Wildlife Society Bulletin* 34:656–663.
- Jessen, R. L. 1981. Special problems with diving ducks. *Proceedings of the International Waterfowl Symposium* 4:139–148.

- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk* 118:557–562.
- Jonsson, J. 1997. Habitat selection studies in avian ecology: a critical review. *Auk* 118:557–562.
- Kaiser, G. W., A. E. Derocher, S. Crawford, M. J. Gill, and I. A. Manley. 1995. A capture technique for Marbled Murrelets in coastal inlets. *Journal of Field Ornithology* 66:321–333.
- Kasischke, E. S., T. S. Rupp, and D. L. Verbyla. 2006. Fire trends in the Alaskan boreal forest. Pp. 285–301 in F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (editors), *Alaska's changing boreal forest*. Oxford University Press, New York, NY.
- Ketterson, E. D., and V. Nolan, Jr. 1983. The evolution of differential bird migration. *Current Ornithology* 1:357–402.
- Klaassen, M., K. F. Abraham, R. L. Jeffries, and M. Vrtiska. 2006. Factors affecting the site of investment, and the reliance on savings for Arctic breeders: the capital-income dichotomy revisited. *Ardea* 94:371–384.
- Korschgen, C. E., K. P. Kenow, A. Gendron-Fitzpatrick, W. L. Green, and F. J. Dein. 1996. Implanting intra-abdominal radio transmitters with external whip antennas in ducks. *Journal of Wildlife Management* 60:132–137.
- LePage, D., G. Gauthier, and S. Menu. 2000. Reproductive consequences of egg-laying decisions in Snow Geese. *Journal of Animal Ecology* 69:414–427.
- Lewis, T. L., D. Esler, W. S. Boyd, and R. Zydalis. 2005. The nocturnal foraging behaviors of wintering Surf Scoters and White-winged Scoters. *Condor* 107:636–646.
- Lindberg, M. S., D. H. Ward, T. L. Tibbetts, and J. Roser. 2007. Winter movement dynamics of black brant. *Journal of Wildlife Management* 71:534–540.
- Linville, R. G., S. N. Luoma, L. Cutter, and G. Cutter. 2002. Increased selenium threat as a result of the invasion of the exotic bivalve *Potamocorbula amurensis* in the San Francisco Bay-Delta. *Aquatic Toxicology* 57:51–64.
- Maisonneuve, C., L. Belanger, D. Bordage, B. Jobin, M. Grenier, J. Beaulieu, S. Gabor, and B. Filion. 2006. American Black Duck and Mallard breeding distribution and habitat relationships along a forest-agriculture gradient in southern Quebec. *Journal of Wildlife Management* 70:450–459.
- Mallory, M. L., P. J. Blancher, P. J. Weatherhead, and D. K. McNichol. 1994. Presence or absence of fish as a cue to macroinvertebrate abundance in boreal wetlands. *Hydrobiologia* 279/280:345–351.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. 2nd ed. Kluwer Academic Publishers, Dordrecht, Netherlands.
- McCarty, J. P. 2001. Ecological consequences of recent climate change. *Conservation Biology* 15:320–331.
- Miller, M. R., J. Y. Takekawa, J. P. Fleskes, D. L. Orthmeyer, M. L. Casazza, and W. M. Perry. 2005. Spring migration of northern pintails from California's Central Valley wintering area tracked with satellite telemetry: routes, timing, and destinations. *Canadian Journal of Zoology* 83:1314–1332.
- Murphy-Klassen, H. M., T. J. Underwood, S. G. Sealy, and A. A. Czyrnyj. 2005. Long-term trends in spring arrival dates of migrant birds at Delta Marsh, Manitoba in relation to climate change. *Auk* 122:1130–1148.
- Newton, I. 1989. *Lifetime reproduction in birds*. Academic Press, London, UK.
- Nichols, F. H., J. E. Cloern, S. N. Luoma, and D. H. Peterson. 1986. The modification of an estuary. *Science* 231:567–573.
- NOAA/NESDIS/OSDPD/SSD. 2006. IMS daily northern hemisphere snow and ice analysis at 4 km and 24 km resolution. National Snow and Ice Data Center, Boulder, CO.
- Nysewander, D. R., J. R. Evenson, B. L. Murphie, and T. A. Cyra. 2004. Trends observed for selected marine bird species during 1993–2002 winter aerial surveys. In T. Droscher and D. A. Fraser (editors), *Proceedings of the Georgia Basin/Puget Sound Research Conference*. <[http://www.psat.wa.gov/Publications/03\\_proceedings/start.htm](http://www.psat.wa.gov/Publications/03_proceedings/start.htm)>.
- Oswood, M. W., N. F. Hughes, and A. M. Milner. 2006. Running waters of the Alaskan boreal forest. Pp. 147–167 in F. S. Chapin III, M. W. Oswood, K. Van Cleve, L. A. Viereck, and D. L. Verbyla (editors), *Alaska's changing boreal forest*. Oxford University Press, New York, NY.
- Payette, S. 2007. Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. *Ecology* 88:770–780.
- Perry, M. C., D. M. Kidwell, A. M. Wells, E. J. R. Lohnes, P. C. Osenton, and S. H. Altmann. 2006. Characterization of breeding habitats for Black and Surf Scoters in the eastern boreal forest and subarctic regions of Canada. Pp. 80–89 in A. Hansen, J. Kerekes, and J. Paquet. *Limnology and waterbirds* 2003. Canadian Wildlife Service Technical Report Series No. 474.
- Petrie, M. J., R. D. Drobney, and D. T. Sears. 2000. Mallard and Black Duck breeding parameters in New Brunswick: a test of the reproductive rate

- hypothesis. *Journal of Wildlife Management* 64: 832–838.
- Prop, J., J. M. Black, and P. Shimmings. 2003. Travel schedules to the high Arctic: Barnacle Geese trade-off the timing of migration with accumulation of fat deposits. *Oikos* 103:403–414.
- Prop, J., and J. Devries. 1993. Impact of snow and food conditions on the reproductive performance of barnacle geese *Branta leucopsis*. *Ornis Scandinavica* 24:110–121.
- R Development Core Team. 2008. R: a language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>>.
- Reed, E. T., G. Gauthier, and J.-F. Giroux. 2004. Effects of spring conditions on breeding propensity of Greater Snow Goose females. *Animal Biodiversity and Conservation* 27:35–46.
- Rempel, R. S., K. F. Abraham, T. R. Gadawski, S. Gabor, and R. K. Ross. 1997. A simple wetland habitat classification for boreal forest waterfowl. *Journal of Wildlife Management* 61:746–757.
- Richardson, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. *Oikos* 30:224–272.
- Robertson, G. J., and F. Cooke. 1999. Winter philopatry in migratory waterfowl. *Auk* 116:20–34.
- Rohwer, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pp. 486–539 in B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu (editors), *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, MN.
- Rosing, M. N., M. Ben-David, and R. P. Perry. 1998. Analysis of stable isotope data: a K nearest-neighbors randomization test. *Journal of Wildlife Management* 62:380–388.
- SAS Institute. 2004. SAS OnlineDoc® 9.1.2. SAS Institute, Inc., Cary, NC.
- Savard, J.-P. L., and P. Lamothe. 1991. Distribution, abundance, and aspects of breeding ecology of Black Scoters, *Melanitta nigra*, and Surf Scoters, *M. perspicillata*, in northern Quebec. *Canadian Field-Naturalist* 105:488–496.
- Savard, J.-P. L., D. Bordage, and A. Reed. 1998. Surf Scoter (*Melanitta perspicillata*). A. Poole and F. Gill (editors), *The birds of North America* No. 363. The Birds of North America, Inc., Philadelphia, PA.
- Schamber, J. L., J. S. Sedinger, D. H. Ward, and K. R. Hagemeyer. 2007. Latitudinal variation in population structure of wintering Pacific Black Brant. *Journal of Field Ornithology* 78:74–82.
- Schilling, M. F. 1986. Multivariate two-sample tests based on nearest neighbors. *Journal of the American Statistical Association* 81:799–806.
- Schmutz, J. A., K. A. Hobson, and J. A. Morse. 2006. An isotopic assessment of protein from diet and endogenous stores: effects on egg production and incubation behavior of geese. *Ardea* 94:385–397.
- Sea Duck Joint Venture (SDJV) Management Board. 2001. Sea Duck Joint Venture strategic plan: 2001–2006. SDJV Continental Team. Unpublished report. USFWS, Anchorage, AK; CWS, Sackville, NB.
- Serreze, M. C., J. E. Walsh, F. S. Chapin III, T. Osterkamp, M. Dyrgerov, V. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry. 2000. Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* 46:159–207.
- Shugart, H. H., R. Leemans, and G. B. Bonan (editors). 1972. *A systems analysis of the global boreal forest*. Cambridge University Press, Cambridge, UK.
- Smith, G. W. 1995. A critical review of the aerial and ground surveys of breeding waterfowl in North America. Biological Science Report 5. National Biological Service, Washington, DC.
- Smol, J. P., and M. S. V. Douglas. 2007. Crossing the final ecological threshold in high Arctic ponds. *Proceedings of the National Academy of Sciences* 104:12395–12397.
- Soja, A. J., N. M. Tchebakova, N. H. F. French, M. D. Flannigan, H. H. Shugart, B. J. Stocks, A. I. Sukhinin, E. I. Parfenova, F. S. Chapin III, and P. W. Stackhouse, Jr. 2007. Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change* 56:274–296.
- Steidl, R. J. 2006. Model selection, hypothesis testing, and risks of condemning analytical tools. *Journal of Wildlife Management* 70:1497–1498.
- Stephens, P. A., S. W. Buskirk, G. D. Hayward, and C. Martinez del Rio. 2005. Information theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology* 42:4–12.
- Traylor, J. J., R. T. Alisauskas, and F. P. Kehoe. 2004. Nesting ecology of White-winged Scoters (*Melanitta fusca deglandi*) at Redberry Lake, Saskatchewan. *Auk* 121:950–962.
- U.S. Fish and Wildlife Service (USFWS). 2002. Waterfowl population status, 2002. U.S. Department of the Interior, Washington, DC.
- Visser, M. E., A. J. Van Noordwijk, J. M. Tinbergen, and C. M. Lessels. 1998. Warmer springs lead to mistimed reproduction in Great Tits (*Parus major*). *Proceedings of the Royal Society of London Series B*, 265:1867–1870.
- Walker, J., M. S. Lindberg, M. C. MacCluskie, M. J. Petruła, and J. S. Sedinger. 2005. Nest survival of

- scaup and other ducks in the boreal forest of Alaska. *Journal of Wildlife Management* 69:582–591.
- Ward, D. H., A. Reed, J. S. Sedinger, J. M. Black, D. V. Derksen, and P. M. Castelli. 2005. North American Brant: effect of changes in habitat and climate on population dynamics. *Global Change Biology* 11:869–880.
- Ward, J. V. 1992. *Aquatic insect ecology, Vol. 1: Biology and habitat*. John Wiley and Sons, Inc., New York, NY.
- Warnock, S. E., and J. Y. Takekawa. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in the San Francisco Bay estuary. *Auk* 112:920–930.
- Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76–83.
- White, G. C., and R. A. Garrott. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, CA.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3:385–397.



