FORAGING EFFORT BY SURF SCOTERS AT THE PERIPHERIES OF THEIR WINTERING DISTRIBUTION: DO FORAGING CONDITIONS INFLUENCE THEIR RANGE?

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ABSTRACT

I measured foraging effort of surf scoters at the northern and southern peripheries of their winter distribution (Southeast Alaska and Baja California, Mexico, respectively), and compared those to foraging effort previously documented at the wintering range core (Strait of Georgia, British Columbia, Canada). I predicted that if foraging conditions influenced their winter distribution, foraging effort would be higher at the peripheries of the distribution and that scoters, which are typically diurnal foragers, might be forced to extend their foraging activities into nocturnal periods. Overall, scoters in Baja California foraged over twice as much as scoters in Alaska, with intermediate foraging effort at the range core. Scoters also foraged nocturnally in Baja California but not in Alaska or British Columbia. I conclude that foraging opportunity may limit winter distribution at the southern periphery, but other factors limit distribution at the northern periphery.

Keywords: Baja California; foraging effort; Juneau; *Melanitta perspicillata;* sea duck; Southeast Alaska; surf scoter; winter distribution; wintering ecology

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CHAPTER 1

General Introduction

1.1 INTRODUCTION

Distributions of animals are affected by a variety of factors, ranging from but not limited to predation danger (Lank et al. 2003, Shervette et al. 2004, Mao et al. 2005), climate, (Walther et al. 2002, Valiela and Bowen 2003, Parmesan 2006, Batalden et al. 2007, Bertin 2008, Eisen et al. 2008, Ward et al. 2009, Boyle 2010), and abundance, quality, and accessibility of food (Johnson and Sherry 2001, Thompson et al. 2005, Copeland et al. 2007, Lindberg et al. 2007, Norris and Martin 2008, Tennent and Downs 2008). Determining factors affecting distribution of migratory birds is particularly challenging, as trade-offs between optimizing survival through increased foraging opportunity or decreased predation risk or exposure to severe weather can change over latitudinal gradients (Ardia 2005, Nebel and Ydenberg 2005) and/or altitudinal gradients (McKinnon et al. 2010); for example, an individual bird migrating to a breeding site further north may ultimately have a lower predation risk at its breeding site, but it is more energetically costly to migrate to that site, and it may encounter more predation and weather events during migration.

A study of altitudinal migration in white-ruffed manikins (*Corapipo altera*), for example, suggests that individuals potentially choose not to migrate from the higher elevation breeding grounds where food is plentiful if they are large enough to successfully fast during long periods of rain. Smaller birds, however, have to migrate to lower elevations despite the plentiful food at the higher breeding elevations, because they are not able to successfully fast during the potential rains of the non-breeding season (Boyle 2008). This is an example of how certain individuals must leave areas of sufficient food due to other risks, thus influencing the distribution of that species. In this case, males are smaller, and therefore more likely to migrate, leading to differential migration by sex; differential migration is common in migratory birds and latitudinal or altitudinal distributions can often be skewed by age and sex classes (Ketterson and Nolan 1976, Cristol et al. 1999, Nebel et al. 2002, Komar et al. 2005, O'Hara et al. 2006).

While it is evident that many factors can affect animal distributions concurrently, food is often an important driver of distribution (Levey and Stiles 1992, Crampton et al. 2011). Ideal free distribution concepts suggest that predator densities should be positively correlated with prey densities (Fretwell and Lucas 1970). Numerous species have been shown to have distributions strongly correlated with food availability at local scales (Murray et al. 1994, Marzluff et al. 1997, O'Donoghue et al. 1998). At larger scales, distributions of species are also often highly correlated with preferred food availability. Black brant (*Branta bernicla*), for example, winter from Baja California up through Alaska along the Pacific coast. While their physiological response to environmental conditions differs between southern and northern sites during the winter, they are consistently associated with eelgrass (*Zostera marina*) beds at the continental scale (Reed et al. 1998, Mason et al. 2006), and the distribution of brant mirrors the range of ice-free eelgrass along the Pacific coast (Green and Short 2003).

Like other animals, sea duck distributions during the non-breeding period have been related to variation in prey resources. Guillemette and Himmelman (1996) found that an increase in numbers of common eiders in the northern Gulf of St. Lawrence, Québec, Canada, did not result in an increase in the number of bivalve food patches used (their primary prey), but rather in increased eider numbers at patches with more food biomass. They suggested that the high level of aggregation was related to high abundance of preferred food resources in some patches and that their distribution closely correlated with the highest density of prey (Guillemette et al. 1993). This study investigates the importance of foraging conditions as a driver of continental winter distribution of another sea duck, the surf scoter (*Melanitta perspicillata*).

1.2 THESIS BACKGROUND

Wintering ecology of surf scoters has been thoroughly studied at the range core in the Strait of Georgia, BC, Canada, (Lewis 2005, Kirk 2007, Kirk et al. 2007, Lewis et al. 2008). These studies indicated that the range core provides high quality foraging habitat for scoters during the winter. However, the wintering range of surf scoters along the Pacific coast extends from Baja California, Mexico through Southcentral Alaska (Savard et al. 1998), and wintering ecology at range peripheries is poorly understood.

I studied wintering ecology of surf scoters at the northern and southern extents of their wintering distribution. Hodges et. al. (2008) estimated that 77,300 scoters (*Melanitta spp.*) winter throughout Southeast Alaska, with the most numerous species being the surf scoter. Conant and Voelzer (unpublished data) recorded thousands of surf scoters along the Baja California coast during the winter, which is an area that historically supported tens of thousands of surf scoters (Saunders and Saunders 1981; Takekawa, unpublished data).

I developed this thesis with the focus of examining factors that may be affecting the winter distribution of this species. Food often influences animal distributions, and Žydelis et al. (2006, 2009) found local scoter winter distributions to be highly correlated with prey abundance; therefore, my question addresses whether food quality, abundance, and accessibility (foraging opportunity) influences surf scoter winter distributions at the continental scale.

1.3 CONSERVATION RATIONALE

Scoter numbers have declined in North America over the past half century (Goudie et al. 1994). Sea ducks are long-lived species with low reproductive rates and they normally do not attempt to breed until 2 to 3 years of age (Ricklefs 1990, Goudie et al. 1994, Savard et al. 1998). Given these life history characteristics, Goudie et al. (1994) suggested that population dynamics of sea ducks are most sensitive to variation in adult survival. Conditions on non-breeding areas, where scoters spend most of their annual cycle, may influence adult survival; therefore, understanding the conditions of these areas, scoter response to these conditions, and whether responses are different among cohorts is important for population conservation.

Differential migration among sex and age classes is common in birds (Cristol et al. 1999, Nebel et al. 2002, Komar et al. 2005, O'Hara et al. 2006), as is differential foraging behavior (Fernández and Lank 2008). Preliminary data indicate that surf scoters exhibit differential migration along the Pacific coast (Iverson 2002). Gaining insight into foraging patterns will help us understand the underlying mechanisms for differential migration and foraging behavior in surf scoters, and whether foraging conditions are a factor driving observed patterns. In turn, this will indicate whether management action aimed at improving foraging conditions at wintering areas might have population-level benefits.

Additionally, studies often focus on measuring daily and/or seasonal energy requirements associated with demands of a particular season (Mason et al. 2006); however, it is likely that an individual's current condition, survival, and reproductive performance are also dictated by cross-seasonal effects (Esler and Grand 1994, Esler et al. 2001, Webster et al. 2002, Anteau and Afton 2004, Petersen and Douglas 2004, Jamieson et al. 2006, Arzel et al. 2007, Norris and Marra 2007, Devries et al. 2008). For surf scoters, these cross-seasonal effects on survival and body condition could be related to foraging conditions at the peripheries of their wintering range, and may be relevant for conservation if certain cohorts are occurring disproportionately at range peripheries.

Finally, climate change is actively affecting distributions of many species (Walther et al. 2002, Valiela and Bowen 2003, Parmesan 2006, Batalden et al. 2007, Eisen et al. 2008, Bertin 2008, Ward et al. 2009); it is essential to understand underlying mechanisms for observed distributions, so that we can predict effects of projected changes to climate.

1.4 THESIS OBJECTIVE

The purpose of this study is to evaluate whether foraging conditions are a primary factor dictating surf scoter wintering distribution throughout their Pacific range. We measured foraging effort at the northern (Juneau, Southeast Alaska, USA) and southern (Baja California, Mexico) peripheries of the surf scoter's wintering distribution. By comparing these data to similar, previously collected data from areas of high quality foraging habitat at the range core (British Columbia, Canada; Kirk et al. 2007, Lewis et al. 2008), we tested predictions stemming from a hypothesis that foraging conditions dictate wintering range, namely that foraging effort will be higher at range peripheries than at the core, including greater proportions of time spent foraging and increased incidence and duration of nocturnal foraging.

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CHAPTER 2

Latitudinal Variation in Foraging Effort of Wintering Surf Scoters

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2.1 INTRODUCTION

Distributions of animals are affected by a variety of factors including inter- and intra-specific competition (Kelly et al. 2003, Fernández and Lank 2006, Dellinger 2007, Hamer et. al 2007), predation danger (Lank et al. 2003, Shervette et al. 2004, Mao et al. 2005), climate (Walther et al. 2002, Valiela and Bowen 2003, Parmesan 2006, Batalden et al. 2007, Bertin 2008, Eisen et al. 2008, Ward et al. 2009, Boyle 2010), disease (Rocke et al. 2005), migration distance (O'Hara et al. 2006), geography (Skagen et al. 2005, Lindsay et al. 2008), and the abundance, quality, and accessibility of food (Johnson and Sherry 2001, Thompson et al. 2005, Copeland et al. 2007, Lindberg et al. 2007, Norris and Martin 2008, Tennent and Downs 2008). Also, these factors may influence age and sex cohorts differently, which in turn may cause cohorts to have different distributions. In migratory birds, season-specific differential effects on cohorts may lead to differential migration, i.e., inter-cohort differences in distributions within a season, which has been observed in many species (Cristol et al. 1999, Nebel et al. 2002, Komar et al. 2005, O'Hara et al. 2006).

Food availability and quality have important influences on animal distributions. Ideal free distribution concepts posed by Fretwell and Lucas (1970) suggest that predator densities should be positively correlated with prey densities. Numerous species have distributions highly correlated with food availability at local scales (Murray et al. 1994, Marzluff et al. 1997, O'Donoghue et al. 1998). At larger scales, distributions also may be highly correlated with preferred food availability. Black brant (*Branta* *bernicla*), for example, winter along the Pacific coast from Baja California to Alaska consistently in association with eelgrass (*Zostera marina*), their primary food (Reed et al. 1998, Mason et al. 2006); brant do not occur outside the range of ice-free eelgrass (Green and Short 2003), suggesting that brant distributions are constrained by eelgrass distributions at the continental scale.

Like other animals, sea duck distributions have been related to variation in prey resources at local scales (Guillemette et al. 1993, Guillemette and Himmelman 1996, Žydelis et al. 2006, 2009). We considered whether foraging conditions influence the wintering distribution of the surf scoter (*Melanitta perspicillata*) at a continental scale. On the Pacific Coast, the surf scoter winter range extends from south coastal Alaska to central Baja California, Mexico (Savard et al. 1998). During winter they feed on a variety of benthic invertebrates (Anderson et al. 2008); bivalves are important prey for surf scoters in many areas (Stott and Olson 1973, Vermeer and Levings 1977) and they often feed on clams in soft-bottom habitats and on mussels in rocky, intertidal areas (Vermeer and Levings 1977, Savard et al. 1998, Lacroix 2001).

Additionally, animals generally show variation in foraging behavior in relation to habitat quality and/or foraging conditions (Pyke et al. 1977, Nummi et al. 2000). Many studies have shown that, in response to declining prey in a particular patch, predators alter their foraging behavior, including increases in allocation of time to foraging (Guillemette et al. 1992, Owen et al. 1992, Monaghan et al. 1994, Davoren 2000, Kirk et al. 2007a). However, variation in foraging behavior at continental scales is less understood.

Foraging conditions encountered by scoters are a composite of food quality, food abundance, and food accessibility; accessibility can be limited by both physical features of the habitat (e.g., soft-bottom areas vs. rocky intertidal areas in marine systems; water depth) and/or temporal features of a particular area (e.g., limited daylength at high latitudes for diurnal foragers during mid-winter). Surf scoters, as with other sea ducks, capture their prey by means of diving. They modify dive frequency and the total amount of time spent feeding depending on quality of foraging habitats and prey abundance (Guillemette et al. 1992, Hario and Ost 2002). Surf scoters can deplete stocks of bivalves throughout the winter (Kirk et al. 2007b, Lewis et al. 2007a) and Kirk et al. (2007a) found that surf scoters responded to declining prey in British Columbia, Canada, by increasing their daily foraging time. Also, Lewis et al. (2007b) reported that when feeding on herring spawn, an ephemerally abundant food source, scoters spent 50% less time foraging than when feeding on bivalves. Therefore, foraging effort (i.e., the amount of time spent feeding) is a good, composite measure of the foraging conditions that a bird is experiencing, as food abundance, quality, and accessibility dictate how much a diving duck is required to forage.

The extent to which scoters feed at night may also be an indicator of foraging conditions. At the core of their winter range, surf scoters forage almost exclusively during the day (Lewis et al. 2005), as do most sea ducks (Nilsson 1970, Goudie and

Ankney 1986, Guillemette et al. 1992, McNeil et al. 1992, Guillemette 1998, Rizzolo et al. 2005). However, if foraging conditions are not adequate for meeting energy needs during daylight hours, sea ducks are known to extend foraging into crepuscular or nocturnal hours (Reed and Flint 2007, Systad et al. 2000, Systad and Bustnes 2001).

We predicted that if foraging conditions constrained the Pacific Coast distribution of wintering surf scoters, scoters at the peripheries of their winter range would (1) spend more of the daylight hours feeding in comparison to birds that winter near the core of the range, and (2) would extend their feeding into nocturnal periods, a behavior not typically observed in the core winter areas (Pyke et al. 1977). If neither of these were observed at the range peripheries, we would infer that factors other than foraging condition influence the distribution of surf scoters. Hence, we examined foraging behavior of surf scoters at the northern and southern extents of their Pacific Coast winter range and contrasted total time of diurnal feeding and extent of nocturnal feeding with that of scoters in the central portion of their winter distribution. We also considered variation in foraging effort within each site, to evaluate effects of environmental conditions and cohort composition, and provide insight into mechanisms leading to observed winter distributions of surf scoters.

2.2 METHODS

2.2.1 Study Areas

We collected data at the northern periphery of the wintering range of surf scoters near Juneau, Alaska, U.S.A. (58.4°N, 134.5°W). Hodges et. al. (2008) estimated that 77,300 scoters (*Melanitta spp.*) winter in Southeast Alaska (hereafter SE Alaska), with surf scoters being the most numerous species. Deep channels and fjords are characteristic of the area; blue mussels (*Mytilus edulis*) are common and widespread in rocky intertidal areas, and constitute the primary prey of surf scoters (J. Hupp, USGS, unpublished data). Predators of surf scoters are widespread throughout the region; bald eagles (*Haliaeetus leucocephalus*) and American mink (*Mustela vison*) commonly depredated and/or scavenged radio-marked surf scoters (this study), and similar predators were documented at the range core (Anderson et al., in press).

We also collected data at the southern periphery of the surf scoter wintering range in Baja California, Mexico (hereafter Baja) in two different bays: Bahía San Quintín (30.5°N, 116.0°W), and Laguna Ojo de Liebre (28.0°N, 114.0°W). These bays support thousands of wintering surf scoters and are characterized by shallow water and intertidal mud flats. Unlike scoters at more northern latitudes, scoters at these sites primarily feed on infaunal invertebrates such as ghost shrimp (*Callianassa spp.*; D. Ward, unpublished data). Contrary to the SE Alaska and core range sites, there are virtually no avian or mammalian predators at these southern wintering sites; bald eagles are extremely rare at the Baja sites and there are no other avian predators (D. Ward, personal communication).

We compared our findings with those from the core of the wintering range (Kirk et al. 2007a, Lewis et al. 2008), represented by two areas in the Strait of Georgia, British Columbia, Canada: the Malaspina Complex (50.0°N, 124.7°W) and Baynes Sound (49.5°N, 124.8°W). The Malaspina Complex is located in the northern Strait of Georgia and includes the waters of the Malaspina, Okeover and Lancelot inlets on mainland British Columbia. Similar to the northern site, this area is characterized by steep fjords and protected inlets with mostly rocky shores and few soft-sediment beaches. Baynes Sound is located on the east shoreline of Vancouver Island and is a shallow coastal channel with many areas of soft-bottom (mud and sand) flats throughout its small, protected bays (Dawe et al. 1998). Previous research (Lewis 2005, Kirk 2007, Kirk et al. 2007a, Lewis et al. 2008) has shown that both of these sites provide high quality foraging habitat for wintering surf scoters. Avian predators, particularly bald eagles, are abundant at these sites.

2.2.2 Diurnal Foraging Effort

We quantified foraging effort by monitoring surf scoter dive behavior via radio telemetry during the winters of 2006/07 and 2007/08 in Baja and during the winters of 2008/09 and 2009/10 in SE Alaska. Surf scoters were captured during the latter half of November and beginning of December at both sites using a modified floating mist net (Kaiser et al. 1995, Brodeur et al. 2008). Methods closely followed those of Lewis et al. (2005, 2007a, 2007b, 2008) and Kirk et al. (2007a, 2008) in British Columbia to allow latitudinal comparisons. We removed captured scoters from nets and placed them in kennels; we processed them on shore or in a laboratory during particularly cold days in SE Alaska. We marked each individual with a USFWS tarsal band and then weighed, determined age class (hatch year [HY] versus after hatch year [AHY] based upon bursal depth; Mather and Esler 1999), and determined sex by plumage of each bird. In Baja, we attached external VHF transmitters to 32 and 37 scoters during 2006 and 2007, respectively, with subcutaneous prongs and glue (Pietz et al. 1995, Iverson et al. 2006, Lewis and Flint 2008). In SE Alaska, we attached VHF transmitters to 50 and 60 scoters during 2008 and 2009, respectively, using the same methods. We distributed radios roughly evenly across sex and age cohorts.

We measured the amount of time scoters spent underwater (hereafter foraging effort) via radio telemetry over the diurnal period, which was defined as the period between sunrise and sunset (for SE Alaska: http://www.usno.navy.mil/USNO/astronomical-applications/data-services/rs-one-year-us; for Baja: http://www.esrl.noaa.gov/gmd/grad/solcalc/). We monitored radio signals from shore when possible and from boat when necessary. A four-element Yagi antennae (Kuechle 2005) connected to an Advanced Telemetry Systems (ATS; Isanti, Minnesota) R4000 receiver and David Clark aviation-grade headsets were used to monitor radios; there was a loss of radio signal when a bird submerged underwater and the signal resumed when the bird arrived back at the surface (Custer et al. 1996). Signal disappearance and reappearance times were recorded to the nearest second during hour-long diurnal monitoring periods. This method accurately documented foraging time, as scoters only dive for their food. Lewis et al. (2005) confirmed that scoters did not engage in surface foraging (e.g., foraging near the surface, especially in shallow water, without submerging the radio antenna, which would underestimate foraging effort) by observing them during foraging bouts during the day. We measured foraging effort for each individual over different tide levels and at various times of day to account for differences in foraging effort due to environmental and/or temporal factors. Overall foraging effort of each individual was an average of its foraging effort at different tide levels and diurnal periods throughout the winter, and is a good composite measure of the effort devoted to foraging during the winter period.

We recognized that foraging effort could be related to environmental factors other than latitude and we documented several attributes during each foraging observation to account for their effects when considering latitudinal variation in foraging effort. For SE Alaska, we considered covariates including: weather (sea state and ambient temperature), time of day, and tide level when examining foraging effort. These have been shown to influence foraging behavior; for example, at higher tides, foraging individuals would be expected to have a fixed increase in dive time to reach their benthic bivalve prey (Paulus 1988, Heath et al. 2008), thus affecting total time foraging during a given monitoring period. For SE Alaska, data on covariates were drawn from existing sources, including tide levels (http://tidesandcurrents.noaa.gov/data_menu.shtml?stn=9452210%20Juneau,%20AK&type=Tide%20Data) and temperature data (http://pajk.arh.noaa.gov/cliMap/climap.php) that were gathered following monitoring periods from the National Oceanic and Atmospheric Administration's (NOAA) data loggers. We did not consider tide, sea state or temperature data in our Baja models, as daily tide fluctuations and temperature variation at these sites were minimal.

2.2.3 Nocturnal Foraging Effort

We estimated the frequency of occurrence and amount of time scoters spent feeding underwater during the night hours, as defined by the period of nocturnal twilight (for SE Alaska: http://www.usno.navy.mil/USNO/astronomical-applications /data-services/rs-one-year-us; for Baja: http://www.esrl.noaa.gov/gmd/grad/solcalc/). Nocturnal twilight occurs when the sun is 12 degrees below the horizon and the horizon, under good atmospheric conditions (e.g., clear skies), is indeterminate. Civil twilight includes the crepuscular period, and we did not consider feeding recorded during that period to be truly nocturnal. We monitored individuals during 30-minute blocks, following a protocol described by Lewis et al. (2005). Due to safety concerns, we typically only monitored nocturnal foraging effort from land; we conducted nocturnal observations from a boat on one calm night (26 February – 27 February 2010).

2.2.4 Data Analyses

All foraging effort summary values (Appendices 1 and 2) were computed using JMP 7 (SAS Institute Inc., 1989-2007) and are presented as mean ± SE; observations were first averaged for each individual and then individual averages were averaged to generate means for both diurnal and nocturnal summaries. Foraging effort variation was evaluated using mixed model repeated measures analyses, which were conducted in program R, version 2.10.1 (The R Foundation for Statistical Computing 2009). We evaluated variation in both minutes underwater per hour and per day in relation to several variables. We estimated minutes underwater per day by multiplying the amount of observed minutes underwater per hour for an individual monitoring period by the amount of daylight hours in the monitoring day. We were interested in both metrics, because hourly foraging rates provide a good estimate for the proportion of time that foraging occurred, while daily foraging rates provides a better estimate of how overall effort may change throughout a winter season. Additionally, the daily foraging effort metric provided a better estimate for how overall effort varied between northern and southern sites, as daylight varied greatly between the sites, and therefore, only looking at hourly foraging rates could prove misleading.

For both northern and southern sites, we had multiple observations for the same radio-marked individuals over the course of each winter. Therefore, we required a mixed modeling procedure to account for these repeated measures of individuals. We used the nlme package (Pinheiro et al. 2009) in R to specify individual as a random effect, and account for individual effects when inferring effects of other variables on foraging effort.

For each response variable, we first ran the most parameterized model in each of the candidate model sets for SE Alaska and Baja using a model with no random effects, a model with a random intercept (which allowed intercept to vary among individuals), and a model with a random intercept and slope (which allowed both intercept to vary among individuals and slope to vary within each individual over DATE). We contrasted Akaike's Information Criteria (AIC; Burnham and Anderson 2002) values among models and found that, for SE Alaska, the random intercept and slope model was the most parsimonious for both hourly (w_i=1.00) and daily (w_i=1.00) foraging effort models; in Baja, the random intercept model was the most parsimonious for both hourly (w_i=0.99) and daily (w_i=0.99) foraging effort models. Proceeding with these best-supported repeated measures structures, we tested the most parameterized model with several feasible correlation structures, and found that for both response variables (minutes underwater per hour and per day), an exponential correlation structure (Pinheiro and Bates 2000) was the best-fitting for SE Alaska; a rational quadratic correlation structure (Pinheiro and Bates 2000) was the best-fitting for the hourly foraging effort response in Baja, while no additional correlation structure was imposed to the Baja daily foraging effort response. Therefore, we applied these respective correlation structures to all of the models in the four candidate model sets described below.

We used an information-theoretic approach to model selection and to draw multi-model inference (Burnham and Anderson 2002). For each of our responses (foraging effort per hour and foraging effort per day), we considered 16 *a priori* candidate models describing different hypotheses about factors influencing foraging effort. We considered the SE Alaska and Baja data sets separately, to minimize the number of candidate models, to generate parameter estimates specific to each site to evaluate sources of local variation, and to generate predicted values that can be contrasted across sites to consider overall differences in foraging effort. We considered both hourly and daily foraging effort, as we were interested in how scoters had to adjust hourly foraging effort throughout the winter, but we also needed a more comparable metric (daily foraging effort) to compare northern and southern sites, considering scoters at southern sites have substantially more daylight hours during the winter to meet their daily energetic needs. We included variables for date effects as date and date^2 terms (referred to collectively as DATE), to allow variation in foraging effort to vary non-linearly over time; for SE Alaska, we adjusted all date values in both years to correspond to 2 December = day 1, and for Baja, we adjusted all date values in both years to correspond to 11 December = day 1.

We considered sex (male or female) and age class (hatch year [HY] or after hatch year [AHY]) together as COHORT, as we hypothesized that these 4 cohorts may respond to environmental pressures differently, and therefore may have differences in foraging effort responses throughout the winter. We included a YEAR term (2008/09 or 2009/10 in SE Alaska; 2006/07 or 2007/08 in Baja) to account for variation between years. In SE Alaska, we considered the following environmental factors (ENVIRON) in each model except for the null: tide height (m), temperature (°C), time of day of observation, and sea state (categorical with three levels—Beaufort Wind Scale 1-4 [low], 5-7 [mid], and 8 [high]). We did this to both limit the number of models in our set, and because we wanted to account for environmental effects that have been previously shown to affect foraging. In Baja, ENVIRON only included a variable for time of day of observation, as the other environmental factors did not vary greatly at these southern sites. Finally, we included the interaction terms COHORT*DATE and COHORT*YEAR in both SE Alaska and Baja data sets, because we hypothesized that the different cohorts might respond to environmental pressures differently both across time within a winter season and between winter seasons.

We constructed the 16 *a priori* candidate model sets for both the SE Alaska and Baja data sets by combining all single-variable models, all combinations of additive models, and the combination of additive models with the two interaction effects singly and the interaction effects combined. We also included a null model (still including random effects) with only an intercept estimated. We included these models (Table 1) because they were all biologically plausible explanations for describing observed foraging effort. We included a null because it was feasible that all scoters foraged at roughly the same rate throughout the winter period and across years.

We calculated Akaike's Information Criterion, adjusted for small sample size (AIC_c), for all models in the candidate model set. We then examined relative support for each model using ΔAIC_c and AIC_c weights (w_i) (Burnham and Anderson 2002). We determined parameter likelihood values by summing the weights of all models that a particular parameter of interest occurred in. We calculated model averaged parameter estimates and unconditional standard errors for all parameters and we used these values as our prediction values.

To evaluate nocturnal foraging effort, we simply tallied the average amount of time underwater per 30-minutes observation block and evaluated the number of observation-blocks that contained nocturnal diving. The total amount of nocturnal foraging was so small, especially in SE Alaska, that there was no reason to further analyze or model those data. In Baja, nocturnal foraging occurred more frequently than in SE Alaska, but was still relatively rare when compared to diurnal foraging.

2.3 RESULTS

2.3.1 Hourly Diurnal Foraging Effort

Surf scoters in SE Alaska foraged an average of 9.4 ± 0.4 minutes per hour (15.7%) from 1 December to 31 March over both study years. The two top models with a modest degree of support included the terms DATE and DATE dependent on COHORT effects. The best supported model from the candidate model set, based on ΔAIC_c and w_i, explaining hourly foraging rate in SE Alaska included terms for DATE, ENVIRONMENT, and the COHORT*DATE interaction, with a w_i of 0.38. The most parameterized model in the candidate model set was supported essentially as well as the top model, with a w_i of 0.36 (Table 1). These two models had over twice the support as the third best supported model (which included terms for YEAR, ENVIRONMENT, and the COHORT*DATE interaction effect), which had a w_i of 0.16. The remaining 13 models had little support.

The DATE parameter had a parameter likelihood of 0.84 and was present in the two top supported models, indicating that DATE was an important parameter explaining variation in time spent foraging during winter (Table 2). The COHORT*DATE interaction effect had a parameter likelihood of 0.98; five models included this parameter in the candidate model set, and these five models ranked as the top five given these data. When the weighted parameter estimates were used to generate predicted values and then plotted, adult males, adult females, and juvenile males had similar foraging rates and similar seasonal variation in foraging rates, with higher effort mid-winter compared to early or late winter. In contrast, juvenile females foraged at higher rates, with dramatic increases in effort during the latter half of the winter (Figure 1).

Overall, scoters in Baja foraged an average of 19.5 ± 1.4 minutes per hour (32.5%), or twice that of scoters in SE Alaska. Foraging effort was similar among all cohorts and both sites (Appendix 2). None of the explanatory terms that we included were well-supported by these data.

We found that the null model (still with a random effect of individual) was the best supported model (w_i = 0.47; Table 3). The next best model (w_i = 0.26) included only the parameter for the start time of observations; the parameter had a negative value, suggesting that hourly foraging rates declined through the course of the observation day. However, the effect size was small relative to the unconditional SE, indicating that this effect was not well supported by these data. The remaining models in the candidate set were not well supported. None of the predictors had high parameter likelihood values (Table 4), which was consistent with our finding that the null model had nearly twice the support based on w_i than the next competing model. This suggests that all cohorts foraged similarly during the course of the winter, and that foraging rates did not vary through winter (Figure 1).

2.3.2 Daily Diurnal Foraging Effort

Scoters in SE Alaska foraged an average of 76.1 ± 3.6 minutes per day from 1 December to 31 March (Appendix 1). Overall, females foraged more than males, particularly during the first winter of study. Given these data and the candidate model set, the most parameterized model was the most parsimonious, with a w_i of 0.41 (Table 1). The second best supported model included the DATE, ENVIRONMENT, and COHORT*DATE parameters, with a w_i of 0.26 (this was the top model when evaluating variation in hourly foraging rate, above). Similar to results from hourly foraging data, the DATE and COHORT*DATE parameters were influential, with parameter likelihoods of

0.90 and 0.97, respectively (Table 2). This indicated that daily foraging effort changed over the course of the winter, and that it did so differently for different cohorts. Predicted values were plotted using weighted parameter estimates (Figure 2), and daily feeding time steadily, and almost linearly, increased through winter for adult males and females and juvenile males, while daily foraging rates increased much more rapidly for juvenile females, especially during the latter half of winter.

Scoters in Baja foraged an average of 214.2 ± 15.4 minutes underwater per day, or nearly 3 times the amount of scoters in SE Alaska (Figure 2). Juvenile birds may have foraged less than adult birds, although precision was low (Appendix 2). Like hourly foraging effort, the best supporting model explaining daily foraging effort given these data and the candidate model set was the null model (with random effects), with a w_i of 0.31 (Table 3). The second best supported model included the observation start time parameter, and had a w_i of 0.28, but the estimate was near zero and had a large unconditional SE (Table 4). The YEAR term appeared in the third best supported model with a w_i of 0.11, but the estimate was -3.40, suggesting that foraging effort by scoters during the second year was 3.4 minutes lower than those during the first year. This effect size was small relative to overall foraging effort, and the unconditional SE was nearly three times the estimate (Table 4).

2.3.3 Nocturnal Foraging Effort

Overall in SE Alaska, based on 287 half-hour monitoring intervals of 55 individuals (*n* = 23 and 32 for years 2008/09 and 09/10, respectively), scoters at night foraged an average of 0.1 ± 0.1 minutes underwater per half-hour (0.3%). Only 32 of the 287 intervals contained at least one dive (11.1%) and even fewer contained more than 2 dives (2.8%); rarely did this diving indicate a foraging bout. We typically were not able to monitor scoters that flew off-shore during the nocturnal period, so we cannot unequivocally conclude that these birds were not diving (although it is unlikely they were foraging off-shore). We were able to monitor 16 off-shore individuals from a boat during the nocturnal period of 26 – 27 February 2010, and we observed no diving for these individuals.

In contrast, in Baja, based on 74 half-hour nocturnal monitoring intervals of 25 individuals (*n* = 11 and 16 for years 2006/07 and 07/08, respectively; two nocturnal foraging males returned the second season), scoters foraged an average of 2.0 ± 0.7 minutes underwater per half-hour (6.8%), and diving was detected during 23% of monitoring periods. Unlike the SE Alaska intervals, those that did contain diving appeared to be legitimate foraging bouts. For example, only considering the nocturnal monitoring periods that contained any presence of diving in Baja (*n* = 17), the mean foraging time of scoters was 9.6 ± 2.0 minutes underwater per half-hour. Hence, as an overall mean, scoters that did forage nocturnally in Baja did so for about a third of the time. These results also suggest that females were foraging nocturnally at higher rates than males; females that fed nocturnally foraged for 14.1 ± 2.5 minutes per half hour (*n* = 7 scoters) compared to 4.4 ± 1.5 minutes per half hour for males (*n* = 6 scoters).

2.4 DISCUSSION

2.4.1 Continental-scale Variation in Foraging Effort

We found that foraging effort of wintering surf scoters varied strongly by latitude, with highest foraging effort observed in Baja, at the southern periphery of their wintering range. On average, surf scoters in SE Alaska foraged less than half the time of surf scoters in Baja during the diurnal period (76 and 214 minutes, respectively), with average foraging time at the range core in British Columbia at an intermediate level (around 100 minutes per day; Kirk et al. 2007a). Similarly, scoters in SE Alaska spent an overall average of 9.4 ± 0.4 minutes per daylight hour in a foraging dive, while those wintering in the range core in B.C., spent an average of around 12 minutes per hour in foraging dives (Kirk 2007a; Lewis et al. 2008). Hourly foraging effort at the southern range periphery in Baja was markedly higher, at 19.5 minutes per hour.

We predicted that if foraging opportunity influenced winter surf scoter distributions, then increased foraging effort would be observed at the range peripheries. However, contrary to that prediction, we found that scoters at their northern wintering periphery in SE Alaska had the lowest foraging effort, calculated at both hourly and daily time scales, indicating that, despite limited day length during midwinter, foraging opportunity in SE Alaska did not limit the winter distribution of scoters. Indeed, mussels were abundant in intertidal zones at the SE Alaska site and wintering scoters there were confirmed to be consuming mussels almost exclusively (J. Hupp, USGS, unpublished data). Additionally, scoters in SE Alaska were heavier than scoters in Baja (D. Esler, Simon Fraser University, unpublished data), despite spending less time feeding, suggesting that Alaskan scoters could attain optimal body mass for local conditions with lower effort than at other wintering sites, further indicating that foraging conditions likely did not constrain the northern wintering distribution.

Data from the southern periphery of the wintering range were consistent with the prediction that foraging opportunity may limit the southern extent of their winter distribution. Despite longer day length, scoters foraged at much higher hourly rates than at the northern periphery and the range core, and consequently invested much more time each day in foraging near the southern periphery. Scoters in Baja foraged on different prey types than at more northern wintering areas, including infaunal invertebrates such as ghost shrimp (*Callianassa spp.*; D. Ward, USGS, unpublished data), which likely influenced their investment in foraging.

We also predicted that if foraging opportunity influenced winter distribution, then scoters would be more likely to extend their foraging effort into nocturnal periods at range peripheries relative to the range core. Lewis et al. (2005) found that scoters wintering at the range core in Baynes Sound, B.C., almost never foraged nocturnally. We rarely observed any incidence of nocturnal diving by scoters in SE Alaska, indicating that their foraging effort was almost exclusively conducted during daylight hours at the northern periphery. In contrast, we found higher incidence of nocturnal foraging at the southern periphery sites in Baja. Consistent with our findings on diurnal foraging, nocturnal foraging observations suggested that foraging opportunity was high at the northern periphery and presumably did not limit the wintering range, while foraging conditions were inferior and potentially limiting at the southern periphery. Findings from past studies indicate that nocturnal foraging in sea ducks is generally observed under extreme situations, such as very short diurnal periods (Systad et al. 2000, Systad and Bustnes 2001, Reed and Flint 2007) or high diurnal predation risk (Merkel and Mosbech 2008).

For foraging opportunity to limit the distribution of wintering scoters, it would have to be so poor as to be unprofitable, potentially leading to effects on physiology or survival if scoters remained. Scoters and other waterfowl are known to respond to reductions in habitat quality by moving to new habitat (e.g., Lovvorn and Gillingham 1996, Kirk et al. 2008), which is likely to occur prior to measurable physiological stress or survival reductions. The regular occurrence of scoters in Baja suggests that this area is a tenable wintering area. However, the observed increases in foraging effort in Baja relative to other parts of their wintering range suggest that habitat quality gets progressively poorer to the south, and that this may explain contemporary winter distributions of the species, at least at the southern periphery. It is unclear what the maximum daily foraging effort of a wintering scoter could be, but it is unlikely that scoters would stay in an area that required foraging effort approaching physiological or behavioral limits.

2.4.2 Temporal Variation in Foraging Effort within Sites

Along with addressing continental scale variation in foraging effort, our data offer insights into factors that influenced foraging effort at local scales. In SE Alaska, daily foraging effort steadily increased through the season for most cohorts, but juvenile female daily investment in foraging increased dramatically over the second half of winter. While these results could be spurious due to limited sample size of juvenile females (*n* = 13 individuals over 2 years; *n* = 7 individuals monitored post-February), the 7 late-season juvenile females all exhibited increased late-season foraging, suggesting that the effect was real. Juvenile females in SE Alaska may have been either (1) more affected by the demands of winter than the other cohorts or (2) unable to equally access prey available to other cohorts.

In regard to hypothesis (1), while there is not great support for a COHORT*YEAR effect, we observed that on average (see Appendix 1), both juvenile and adult females foraged somewhat more during the first, colder and harsher season (ambient mean temperature of -4.2$^{\circ C}$ and 440.7cm of snow between December 2008 and 30 March 2009; mean of -0.3$^{\circ C}$ and 103.6cm of snow between December 2009 and 30 March 2010). Female scoters are considerably smaller and lighter than male scoters (D. Esler, Simon Fraser University, unpublished data), and have a larger ratio of surface area to body mass, resulting in higher mass-specific thermoregulatory costs, which may affect their energy requirements and subsequent foraging effort. Fischer and Griffin (2000) observed that female harlequin ducks (*Histrionicus histrionicus*) at Shemya Island, Alaska, had higher foraging rates than males, and postulated it was due to an increased need to fulfill energetic demands due to greater heat loss caused by cold weather. Our data (Figures 1 and 2) and those from Baynes Sound, B.C., suggested that females foraged more, on average, than males during winter, consistent with the hypothesis of higher mass-specific energetic costs. In regard to hypothesis (2), females have smaller feather free bills and bill widths than males (D. Esler, Simon Fraser University, unpublished data), which may constrain the size classes of prey they can consume (Iverson 2002). As winter progressed, preferred, smaller sizes of mussels may have been depleted (see Kirk et al. 2007a), leaving larger sizes of mussel stocks for the remainder of the winter. Females (and especially inexperienced juvenile females) may have been unable to remove or consume larger size classes that remained available for other cohorts, resulting in higher foraging effort for females.

Across all cohorts, daily foraging effort increased considerably through winter in SE Alaska (Figure 2). This may have resulted from depletion of finite stocks of mussels, their primary prey, which has been observed in numerous other studies. For example, common eiders have been shown to substantially deplete mussel beds over the course of a winter (Guillemette et. al. 1996). Similarly, Kirk et al. (2007a) observed that scoters wintering in BC foraged at higher daily rates in March (154 ± 14 minutes) than in

December (64 ± 5 minutes). They hypothesized that this increase in feeding time was almost certainly a product of declining food resources. We observed mussel beds in SE Alaska that had been completely depleted, consistent with the hypothesis that increased foraging effort at the northern periphery through winter was due to a decrease in available food.

In contrast to data from SE Alaska, we did not observe within-site variation in foraging effort in Baja related to date, cohort, site, or year. This suggests consistent foraging conditions, with subsequent stable foraging effort (though markedly higher than wintering areas at higher latitudes). The climate in Baja is warmer with fewer drastic weather events relative to more northern sites and day length is longer and changes less throughout the winter, providing scoters at southern sites with a more stable and predictable environment, all of which may contribute to observed lack of variation.

Environmental factors such as weather, time of day, and tide did not have strong effects at either the southern or northern periphery. Other studies of sea ducks in areas with large tidal fluctuations have documented decreases in foraging effort during higher tides, presumably to reduce the amount of fixed travel time to foraging patches and as a by-product of a decrease in foraging bout duration and total number of dive cycles due to greater dive durations (Systad and Bustnes 2001, Heath et. al. 2008); however, these studies have also documented high overall foraging effort. In contrast, Reed and Flint (2007) reported that both Steller's eiders and harlequin ducks near Dutch Harbor, Alaska, had much lower foraging rates than sea ducks elsewhere and foraged throughout the day, even at higher tides. They suggested that due to high food availability, energetic constraints were minimal, and therefore the ducks were not forced to make as drastic diving alterations or timing concessions to their foraging schedule when compared to ducks in other studies that were energetically constrained. Similarly, our data suggest that this is occurring in SE Alaska.

2.4.3 Differential Migration and Trade-Offs Among Wintering Sites

Given that winter foraging conditions were better for scoters in SE Alaska than in other sites farther south, there must be plausible explanations for why some birds wintered elsewhere. Choice of a wintering site presumably represents a balance of costs and benefits, and the optimal solution may differ among individuals. For example, costs and benefits of different wintering conditions can vary by cohort, and differential migration among sex and age classes is a common phenomenon in migratory birds (Cristol et al. 1999, Nebel et al. 2002, Komar et al. 2005, O’Hara et al. 2006). Data from Iverson (2002) indicate that scoters exhibit differential migration along the Pacific coast. Based on surveys, higher proportions of males and adults winter at more northern latitudes, while higher proportions of females and juveniles winter at more southern latitudes (D. Esler, Simon Fraser University, unpublished data).

Our foraging data may help explain observed differential migration in surf scoters. Although foraging effort was generally lower in Alaska, suggesting better foraging conditions, juvenile females exhibited high foraging effort, suggesting that they did not benefit from foraging opportunities to the same degree as other cohorts. At more southerly latitudes, differential foraging effort did not exist, suggesting that the associated costs/benefits of those wintering sites were not cohort dependent.

Factors other than foraging effort likely influenced the cost/benefit balance for choice of wintering sites. For example, winter survival in SE Alaska was lower than at sites in B.C. or in Baja (B. Uher-Koch, Simon Fraser University, personal communication*)*, and this was particularly true for juvenile cohorts. We speculate that this may have been due to higher thermoregulatory costs for smaller-bodied individuals, or increased predation on inexperienced birds. We suggest that larger (males) and more experienced (adults) birds may choose to winter in SE Alaska because they benefit from good foraging conditions and because they are less vulnerable to mortality risks than other cohorts. Smaller (females) and less experienced (juveniles) birds may choose to winter further south where, although foraging conditions are not as good, they trade-off increases in foraging effort against reduced mortality risk, resulting in latitudinal clines in age and sex ratios.

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Table 1. General linear mixed model selection results assessing variation in both hourly and daily foraging effort of radio-marked surf scoters in SE Alaska, 2008-2010, based on 959 hour-long monitoring periods (N). Candidate models are presented in order of ΔAIC_c and weight (w_i), and the number of parameters in each model is specified (k). DATE (date+date^2) is in unit days and scaled so that 2 December = day 1. COHORT is a categorical variable (AHYF = adult female; AHYM = adult male; HYF = juvenile female; HYM = juvenile male) with adult female as the reference value. YEAR is a categorical value (2008/09 and 2009/10) with 2008/09 as the reference value. ENVIRON includes sea state, tide height (m), ambient temperature (°C) and observation start time. Sea state is a categorical value (Beaufort [low] 1-4, [medium] 5-7, [high] 8) with Beaufort 1-4 as the reference value. Observation start time is measured in time of day, with midnight represented as 00:00:00. The asterisk represents interaction effects between COHORT and DATE, and COHORT and YEAR; the AHYF*DATE and AHYF*YEAR interactions are reference values.

		Minutes Underwater/Hr					Minutes Underwater/Day		
Model	N	k	ΔAICc	w_i	Model	N	k	ΔAICc	w_i
Date + Environ + Cohort*Date	959	22	0.00	0.38	Date + Cohort + Year + Environ + Cohort*Date + Cohort*Year	959	29	0.00	0.41
Date + Cohort + Year + Environ + Cohort*Date + Cohort*Year	959	29	0.12	0.36	Date + Environ + Cohort*Date	959	22	0.92	0.26
Year + Environ + Cohort*Date	959	23	1.72	0.16	Date + Cohort + Environ + Cohort*Date	959	25	2.00	0.15
Date + Cohort + Environ + Cohort*Date	959	25	3.88	0.06	Year + Environ + Cohort*Date	959	23	2.92	0.10
Date + Cohort + Year + Environ + Cohort*Date	959	26	5.82	0.02	Date + Cohort + Year + Environ + Cohort*Date	959	26	4.07	0.05
Date + Cohort + Environ + Cohort*Year	959	23	8.36	0.01	Date + Environ	959	16	6.90	0.01
Date + Environ	959	16	8.65	0.01	Date + Cohort + Environ + Cohort*Year	959	23	7.57	0.01
Date + Year + Environ	959	17	10.28	0.00	Date + Year + Environ	959	17	8.95	0.00
Date + Cohort + Environ	959	19	11.29	0.00	Date + Cohort + Environ	959	19	10.82	0.00
Null	959	9	12.47	0.00	Date + Cohort + Year + Environ	959	20	12.89	0.00
Date + Cohort + Year + Environ	959	20	13.05	0.00	Null	959	9	43.25	0.00
Cohort + Environ + Cohort*Year	959	21	14.79	0.00	Cohort + Environ + Cohort*Year	959	21	44.85	0.00
Environ	959	14	14.82	0.00	Environ	959	14	45.44	0.00
Year + Environ	959	15	16.54	0.00	Year + Environ	959	15	47.56	0.00
Cohort + Environ	959	17	17.85	0.00	Cohort + Environ	959	17	50.05	0.00
Cohort + Year + Environ	959	18	19.74	0.00	Cohort + Year + Environ	959	18	52.04	0.00

Table 2. Parameter likelihoods, weighted parameter estimates and associated unconditional standard errors from general linear mixed models assessing variation in both hourly and daily foraging effort in radio-marked surf scoters in SE Alaska, 2008-2010. Parameter estimates for DATE (date+date^2) are in unit days and scaled so that 2 December = day 1. COHORT is a categorical variable (AHYF = adult female; AHYM = adult male; HYF = juvenile female; HYM = juvenile male) with adult female as the reference value. YEAR is a categorical value (2008/09 and 2009/10) with 2008/09 as the reference value. Sea state is a categorical value (Beaufort [low] 1-4, [medium] 5-7, [high] 8) with Beaufort 1-4 as the reference value. Tide is measured in meters (m), temperature is measured in degrees Celsius (°C), and observation start time is measured in time of day, with midnight represented as 00:00:00. The asterisk represents interaction effects between COHORT and DATE, and COHORT and YEAR; the AHYF*DATE and AHYF*YEAR interactions are reference values. Parameter estimates close to 1.0 signify explanatory variables with the greatest relative support.

		Minutes Underwater/Hr			**Minutes Underwater/Day**		
Parameter		Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE	Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE
Intercept		1.00	7.078	2.476	1.00	41.366	19.948
DATE		0.84			0.90		
	Date		0.078	0.051		0.696	0.478
	Date^2		-0.0006	0.0005		-0.0004	0.0050
COHORT		0.45			0.63		
	AHYM		-2.600	3.592		-21.543	28.445
	HYF		2.859	4.170		33.555	36.960
	HYM		-2.650	3.843		-18.716	29.601
YEAR		0.55			0.57		
	Year		-0.613	1.220		-6.260	10.128
ENVIRON		1.00			1.00		
	Tide		0.132	0.090		1.048	0.823
	Temp		-0.008	0.040		-0.177	0.366
	Sea (Beaufort 5-7)		0.615	2.211		3.393	20.320
	Sea (Beaufort 8)		3.577	1.981		34.853	18.218
	Observation Start Time		0.097	0.069		0.992	0.638
COHORT*DATE		0.98			0.97		
	AHYM*Date		-0.029	0.066		-0.334	0.597
	HYF*Date		-0.203	0.090		-2.409	1.009
	HYM*Date		-0.034	0.071		-0.434	0.653
	AHYM*Date^2		0.0003	0.0006		0.0039	0.0061
	HYF*Date^2		0.0030	0.0009		0.0343	0.0100
	HYM*Date^2		0.0003	0.0007		0.0042	0.0066

Table 2 continued

	Minutes Underwater/Hr			Minutes Underwater/Day		
Parameter	Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE	Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE
COHORT*YEAR	0.37			0.42		
AHYM*Year		1.285	1.868		11.367	15.487
HYF*Year		-1.166	1.886		-9.241	14.943
HYM*Year		1.574	2.227		12.789	17.297

Table 3. General linear mixed model selection results assessing variation in both hourly and daily foraging effort of radio-marked surf scoters in Baja California, Mexico, 2006-2008, based on 239 hour-long monitoring periods (N). Candidate models are presented in order of ΔAIC_c and weight (w_i), and the number of parameters in each model is specified (k). DATE (date+date^2) is in unit days and scaled so that 11 December = day 1. COHORT is a categorical variable (AHYF = adult female; AHYM = adult male; HYF = juvenile female; HYM = juvenile male) with adult female as the reference value. YEAR is a categorical value (2006/07 and 2007/08) with 2006/07 as the reference value. ENVIRON includes observation start time; observation start time is measured in time of day, with midnight represented as 00:00:00. The asterisk represents interaction effects between COHORT and DATE, and COHORT and YEAR; the AHYF*DATE and AHYF*YEAR interactions are reference values.

		Minutes Underwater/Hr					Minutes Underwater/Day		
Model	N	k	ΔAICc	w_i	Model	N	k	ΔAICc	w_i
Null	239	4	0.00	0.47	Null	239	3	0.00	0.31
Environ	239	5	1.19	0.26	Environ	239	4	0.18	0.28
Year + Environ	239	6	2.85	0.11	Year + Environ	239	5	1.97	0.11
Date + Environ	239	7	4.64	0.05	Date + Environ + Cohort*Date	239	12	2.47	0.09
Cohort + Environ	239	8	4.95	0.04	Cohort + Environ	239	7	3.30	0.06
Date + Year + Environ	239	8	6.41	0.02	Year + Environ + Cohort*Date	239	13	3.77	0.05
Date + Environ + Cohort*Date	239	13	6.56	0.02	Date + Environ	239	6	4.03	0.04
Cohort + Year + Environ	239	9	6.72	0.02	Cohort + Year + Environ	239	8	5.21	0.02
Year + Environ + Cohort*Date	239	14	8.05	0.01	Date + Year + Environ	239	7	5.75	0.02
Date + Cohort + Environ	239	10	8.47	0.01	Date + Cohort + Environ	239	9	7.11	0.01
Cohort + Environ + Cohort*Year	239	12	9.97	0.00	Date + Cohort + Environ + Cohort*Date	239	15	7.90	0.01
Date + Cohort + Year + Environ	239	11	10.33	0.00	Cohort + Environ + Cohort*Year	239	11	8.35	0.00
Date + Cohort + Environ + Cohort*Date	239	16	12.01	0.00	Date + Cohort + Year + Environ	239	10	8.96	0.00
Date + Cohort + Environ + Cohort*Year	239	14	13.48	0.00	Date + Cohort + Year + Environ + Cohort*Date	239	16	9.15	0.00
Date + Cohort + Year + Environ + Cohort*Date	239	17	13.53	0.00	Date + Cohort + Year + Environ + Cohort*Date + Cohort*Year	239	19	10.78	0.00
Date + Cohort + Year + Environ + Cohort*Date + Cohort*Year	239	20	14.70	0.00	Cohort + Environ + Cohort*Year	239	13	12.34	0.00

Table 4. Parameter likelihoods, weighted parameter estimates and associated unconditional standard errors from general linear mixed models assessing variation in both hourly and daily foraging effort in radio-marked surf scoters in Baja California, Mexico, 2006-2008. Parameter estimates for DATE (date+date^2) are in unit days and scaled so that 11 December = day 1. Cohort is a categorical variable (AHYF = adult female; AHYM = adult male; HYF = juvenile female; HYM = juvenile male) with adult female as the reference value. Year is a categorical value (2006/07 and 2007/08) with 2006/07 as the reference value. Observation start time is measured in time of day, with midnight represented as 00:00:00. The asterisk represents interaction effects between COHORT and DATE, and COHORT and YEAR; the AHYF*DATE and AHYF*YEAR interactions are reference values. Parameter estimates close to 1.0 signify explanatory variables with the greatest relative support.

		Minutes Underwater/Hr			**Minutes Underwater/Day**		
Parameter		Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE	Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE
Intercept		1.00	20.597	4.077	1.00	254.589	60.586
DATE		0.09			0.17		
	Date		0.002	0.013		0.145	0.442
	Date^2		-0.00003	0.00013		-0.001	0.004
COHORT		0.07			0.11		
	AHYM		0.200	0.482		3.849	9.081
	HYF		-0.102	0.349		-1.739	6.273
	HYM		-0.171	0.462		-3.697	9.366
YEAR		0.16			0.21		
	Year		-0.240	0.631		-3.402	9.095
ENVIRON		0.53			0.69		
	Observation Start Time		-0.183	0.300		-4.243	4.696
COHORT*DATE		0.03			0.15		
	AHYM*Date		0.000	0.005		-0.008	0.290
	HYF*Date		-0.005	0.011		-0.226	0.508
	HYM*Date		0.006	0.014		0.400	0.806
	AHYM*Date^2		0.00001	0.00006		0.001	0.004
	HYF*Date^2		0.00005	0.00011		0.003	0.005
	HYM*Date^2		-0.00009	0.00019		-0.005	0.010

Table 4 continued

	Minutes Underwater/Hr			Minutes Underwater/Day		
Parameter	Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE	Parameter Likelihood	Weighted Parameter Estimate	Unconditional SE
COHORT*YEAR	0.00			0.01		
AHYM*Year		-0.016	0.043		-0.152	0.597
HYF*Year		0.020	0.046		0.456	1.034
HYM*Year		-0.004	0.028		-0.344	0.861

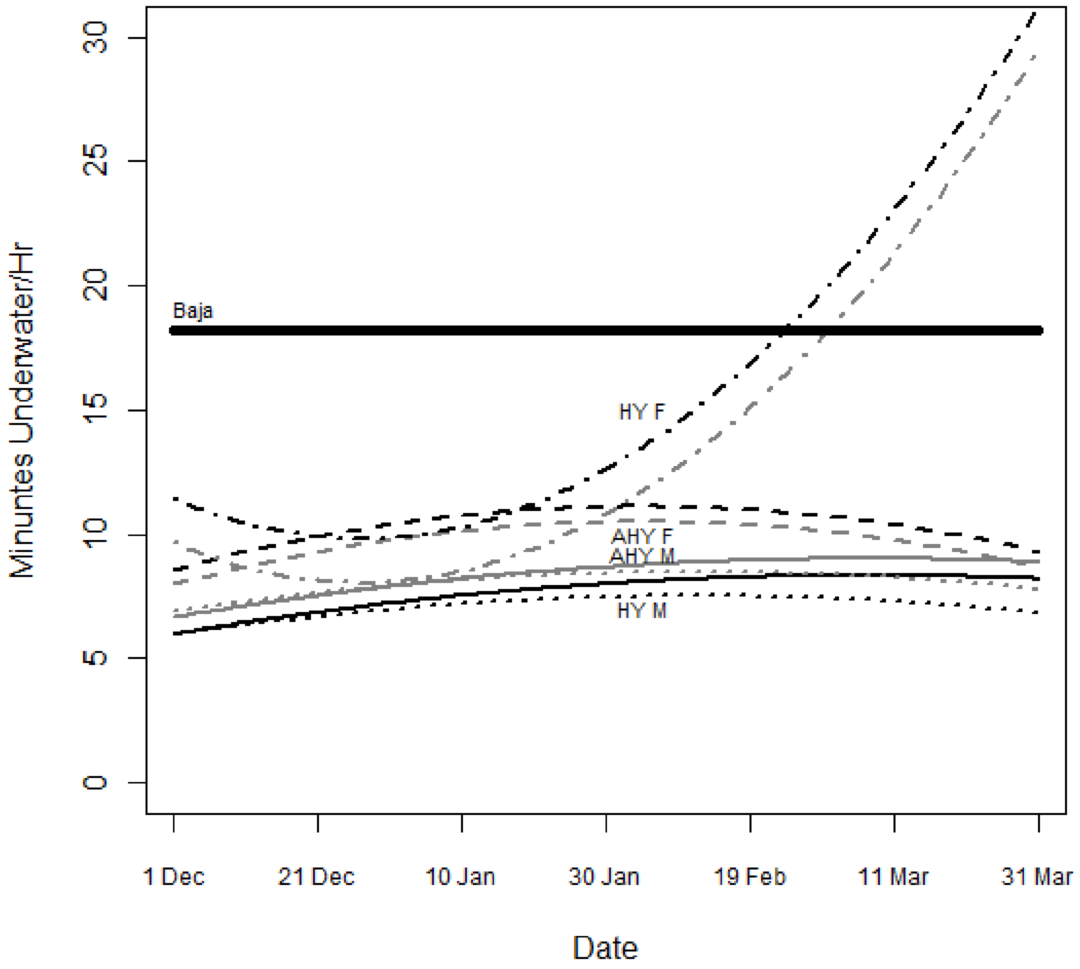

Figure 1. Hourly foraging effort of surf scoters at the peripheries of their winter range from 1 December through 31 March. SE Alaska predictions are based on the most parameterized model using the weighted parameter estimates. Adult females (AHYF), adult males (AHYM), juvenile females (HYF) and juvenile males (HYM) in SE Alaska are represented by the following line styles, respectively: dash, solid, dot-dash, dot; the black and gray lines correspond to the years 2008/09 and 2009/10, respectively, in SE Alaska. The Baja estimate is derived from the intercept for the null (best supported) model and is representative of both winter seasons.

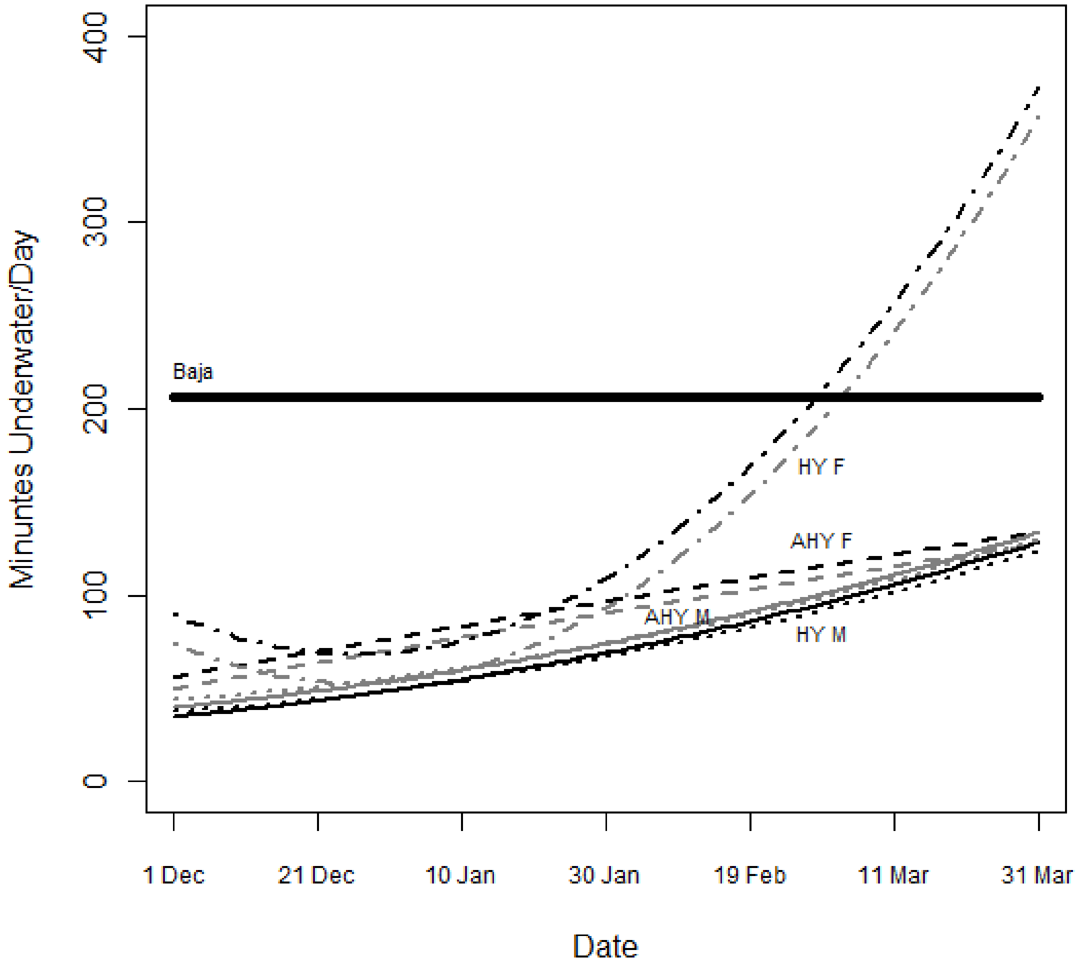

Figure 2. Daily foraging effort of surf scoters at the peripheries of their winter range from 1 December through 31 March. SE Alaska predictions are based on the most parameterized model using the weighted parameter estimates. Adult females (AHYF), adult males (AHYM), juvenile females (HYF) and juvenile males (HYM) in SE Alaska are represented by the following line styles, respectively: dash, solid, dot-dash, dot; the black and gray lines correspond to the years 2008/09 and 2009/10, respectively, in SE Alaska. The Baja estimate is derived from the intercept for the null (best supported) model and is representative of both winter seasons.

CHAPTER 3

General Conclusions

3.1 GENERAL CONCLUSIONS

Wintering ecology of surf scoters has been studied intensively in British Columbia, Canada, at the Pacific wintering range core (Iverson 2002; Kirk 2007; Kirk et al. 2007a, 2007b, 2008; Lewis et al. 2005, 2007a, 2007b, 2008; and Žydelis et al. 2006, 2009). These studies support the conclusion that the range core provides high quality foraging habitat for wintering surf scoters. However, during the winter scoters are distributed from Baja California at the southern periphery through Southeast Alaska (and at lower densities in Southcentral Alaska and the Aleutians, at latitudes similar to or lower than the Juneau site in SE Alaska). Given this, and knowing that high quality foraging opportunity was available for scoters at the range core, I conducted this study to determine factors that may be limiting winter distribution at range peripheries, with an emphasis on investigating whether foraging opportunity was a limiting factor.

I predicted that scoters would forage more at the range peripheries if foraging opportunity was a limiting factor. This study revealed that foraging effort of wintering surf scoters varied strongly by latitude, with highest foraging effort observed in Baja, at the southern periphery of their wintering range. On average, surf scoters in SE Alaska foraged less than half the time of surf scoters in Baja during the course of a day (76 and 214 minutes, respectively), with average foraging time at the range core in British Columbia at an intermediate level (around 100 minutes per day; Kirk et al. 2007a). Similarly, scoters in SE Alaska spent an overall average of 9.4 ± 0.4 minutes per daylight hour in a foraging dive, while those wintering in the range core in B.C. spent an average of around 12 minutes per hour in a foraging dive (Kirk 2007a; Lewis et al. 2008). Hourly foraging effort at the southern range periphery in Baja was markedly higher, at 19.5 minutes per hour. Given these results, I inferred that foraging opportunity may be limiting at the southern periphery, but that scoters are not required to invest as much time in foraging at the northern periphery when compared to foraging scoters at more southern latitudes.

I also predicted that if foraging opportunity limited winter distribution, then scoters (typically diurnal foragers) would be more likely to extend their foraging effort into nocturnal periods at range peripheries relative to the range core. Other studies of sea ducks (eiders, specifically) at high latitudes during winter reported on incidence of nocturnal foraging due to limited daylight period (Systad et al. 2000, Systad and Bustnes 2001, Reed and Flint 2007). However, Lewis et al. (2005) found that scoters wintering at the range core in Baynes Sound, B.C., almost never foraged nocturnally, further indicating that coastal B.C. provides high quality foraging habitat. Likewise, I rarely observed nocturnal diving by scoters in SE Alaska, indicating that their foraging effort was almost exclusively conducted during daylight hours at the northern periphery. In contrast, I found higher incidence of nocturnal foraging at the southern periphery sites in Baja. Consistent with my findings on diurnal foraging, evidence from nocturnal foraging observations suggested that foraging opportunity was high at the northern periphery and presumably did not limit the wintering range, while foraging conditions were inferior and potentially limiting at the southern periphery.

These results also indicate that cohort responses to environmental pressures and diminishing food resources throughout the winter can differ dramatically. These foraging data, therefore, may help explain observed differential migration (Iverson et al. 2002; D. Esler, Simon Fraser University, unpublished data) in surf scoters. Although foraging effort was generally lower in Alaska, suggesting better foraging conditions, juvenile females exhibited high foraging effort, suggesting that they did not benefit from foraging opportunities to the same degree as other cohorts. At more southerly latitudes, differential foraging effort did not exist, suggesting that the associated costs/benefits of those wintering sites were not cohort dependent.

There were additional differential costs of winter site choice across cohorts. Specifically, winter survival in SE Alaska was lower than at sites in B.C. or in Baja (B. Uher-Koch, Simon Fraser University, personal communication), and this was particularly true for juvenile cohorts. I speculate that this may have been due to higher thermoregulatory costs for smaller-bodied individuals, or increased predation on inexperienced birds, as there was a greater incidence of mortality of juveniles in SE Alaska than of adults. I suggest that larger (males) and more experienced (adults) birds may choose to winter in SE Alaska because there are good foraging conditions and because they are less vulnerable to mortality risks than other cohorts. Smaller (females) and less experienced (juveniles) birds may choose to winter further south where, although foraging conditions are not as good, they trade-off increases in foraging effort against reduced mortality risk, resulting in latitudinal clines in age and sex ratios.

This observation of differential migration in relation to foraging opportunity trade-offs has important implications for conservation. It is evident that conservation efforts to increase food availability in SE Alaska for wintering scoters is not necessary, as food is plentiful; lower winter survival in SE Alaska is likely due to weather conditions and predation, both of which are difficult to address in regards to lowering the risks of those factors via management actions. In contrast, management actions aimed at increasing foraging opportunity at the southern periphery, where more females and juveniles are wintering, may in fact benefit those wintering scoters, ensuring that more females are fit to breed upon arrival to the breeding grounds in the spring.

I suggest that further research should more thoroughly address age/sex ratios at sites in the northern and southern peripheries, to further clarify the extent of differential migration. With this information, managers could better address issues affecting specific age/sex classes at different areas of the winter range along the latitudinal cline. Additionally, surf scoters, like other waterfowl, often have male-biased sex ratios (Bellrose 1961) and therefore their population dynamics are driven by the vital rates of females. Further research and management action should recognize that conservation efforts directed at adult females has the largest effects, and knowledge of differential migration and factors underlying this phenomenon may contribute to improving management efforts.

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FORAGING SUMMARY APPENDICES

Appendix 1. Southeast Alaska foraging effort summary (mean ± SE).

	# of Individuals	*# of Obs.*	Dives/Hr	SE	Dive Duration (Seconds)	SE	Minutes Underwater/ Hr	SE	Minutes Underwater/ Day	SE
Overall	70	970	22.9	1.1	26.1	0.7	9.4	0.4	76.1	3.6
Overall 2008	33	361	26.2	1.7	22.8	0.7	9.5	0.7	74.7	4.5
Overall 2009	37	609	19.9	1.2	29.0	0.8	9.2	0.5	77.3	5.6
AHY F	18	238	26.8	2.8	24.6	1.2	10.2	1.0	83.6	8.0
AHY F 2008	7	74	34.9	4.8	21.1	1.5	11.8	2.1	95.4	12.7
AHY F 2009	11	164	21.7	2.3	26.7	1.3	9.2	1.0	76.1	10.1
AHY M	21	351	20.9	1.4	26.3	1.3	8.8	0.6	71.1	5.3
AHY M 2008	11	178	21.7	1.6	23.6	1.4	8.3	0.8	68.4	6.1
AHY M 2009	10	173	20.0	2.5	29.2	1.8	9.3	1.0	74.1	9.2
HY F	13	128	21.7	3.1	29.6	1.5	9.9	1.1	82.0	11.9
HY F 2008	4	16	33.9	4.3	24.1	2.3	12.4	1.0	93.3	7.9
HY F 2009	9	112	16.4	2.4	32.0	1.3	8.8	1.4	76.9	17.0
HY M	18	253	22.0	1.5	24.8	1.1	8.8	0.6	70.1	4.8
HY M 2008	11	93	22.3	2.1	22.6	1.2	8.3	0.9	61.1	5.0
HY M 2009	7	160	21.6	2.0	28.4	1.1	9.7	0.6	84.1	7.2

Appendix 2. Baja California foraging effort summary (mean ± SE).

	# of Individuals	*# of Obs.*	Dives/Hr	SE	Dive Duration (Seconds)	SE	Minutes Underwater/ Hr	SE	Minutes Underwater/ Day	SE
Overall	39	240	36.6	3.4	31.8	2.1	19.5	1.4	214.2	15.4
Overall 2007[1]	27	156	37.6	4.2	31.9	2.7	20.2	1.9	218.7	19.6
Overall 2008[1]	15	84	31.6	5.4	33.5	3.0	17.0	1.9	192.9	22.6
Overall BSQ	22	161	37.4	4.5	29.2	2.6	18.9	1.7	210.1	17.2
Overall ODL	17	79	35.6	5.4	35.1	3.4	20.2	2.5	219.6	27.9
AHY Female	12	75	42.9	5.6	25.9	2.6	19.1	1.6	211.0	16.4
AHY Female 2007	9	54	39.3	6.2	27.7	3.3	19.9	2.0	220.0	20.6
AHY Female 2008	3	21	53.5	12.3	20.3	1.4	16.7	2.2	183.9	17.5
AHY Female BSQ	8	62	41.6	5.7	22.5	1.0	18.4	1.0	208.8	11.3
AHY Female ODL	4	13	45.4	13.8	32.6	7.0	20.5	4.8	215.2	48.3
AHY Female BSQ 2007	5	41	34.5	3.2	23.9	1.0	19.4	0.8	223.8	10.8
AHY Female BSQ 2008	3	21	53.5	12.3	20.3	1.4	16.7	2.2	183.9	17.5
AHY Female ODL 2007	4	13	45.4	13.8	32.6	7.0	20.5	4.8	215.2	48.3
AHY Female ODL 2008	0	0								
AHY Male	11	70	29.8	5.8	38.2	3.9	21.0	3.3	231.5	36.6
AHY Male 2007[2]	7	40	37.6	7.6	39.5	4.9	23.8	4.1	255.9	43.8
AHY Male 2008[2]	6	30	14.9	2.9	39.2	5.1	13.9	3.9	159.5	47.8
AHY Male BSQ	5	36	25.1	4.9	41.4	7.4	17.3	3.7	188.4	36.2
AHY Male ODL	6	34	33.7	10.1	35.6	4.1	24.2	5.3	267.5	59.0
AHY Male BSQ 2007[2]	3	21	32.6	3.1	42.5	12.5	23.3	3.5	251.2	33.4
AHY Male BSQ 2008[2]	3	15	16.1	5.5	42.8	5.8	10.9	2.7	121.1	25.9

Appendix 2 continued

	# of Individuals	*# of Obs.*	Dives/Hr	SE	Dive Duration (Seconds)	SE	Minutes Underwater/ Hr	SE	Minutes Underwater/ Day	SE
AHY Male ODL 2007[2]	4	19	43.1	12.9	36.8	1.7	25.4	7.1	271.9	77.3
AHY Male ODL 2008[2]	3	15	13.6	3.0	35.6	9.2	16.9	7.6	197.8	96.3
HY Female	12	64	34.2	5.6	33.2	4.5	17.8	2.3	198.5	25.6
HY Female 2007	6	31	31.0	8.9	32.1	8.9	15.3	3.9	166.2	42.0
HY Female 2008	6	33	37.4	7.5	34.3	3.3	20.3	2.4	230.8	26.6
HY Female BSQ	7	47	34.3	7.1	29.2	4.3	18.1	2.8	205.0	29.6
HY Female ODL	5	17	34.0	10.1	38.8	9.2	17.4	4.4	189.4	49.6
HY Female BSQ 2007	2	20	26.0	11.6	20.5	12.3	15.2	8.8	177.5	100.2
HY Female BSQ 2008	5	27	37.7	9.1	32.7	3.5	19.3	2.7	216.0	27.1
HY Female ODL 2007	4	11	33.5	13.0	37.8	11.8	15.4	5.0	160.5	52.0
HY Female ODL 2008	1	6	35.8		42.7		25.3		304.9	
HY Male[3]	5	31	41.0	15.0	29.0	4.1	20.6	6.2	217.4	62.2
HY Male 2007	5	31	41.0	15.0	29.0	4.1	20.6	6.2	217.4	62.2
HY Male 2008	0	0								
HY Male BSQ	3	16	51.3	24.7	28.5	4.9	24.4	10.0	255.3	101.0
HY Male ODL	2	15	25.6	4.9	29.8	9.8	15.0	5.1	160.5	51.3
HY Male BSQ 2007	3	16	51.3	24.7	28.5	4.9	24.4	10.0	255.3	101.0
HY Male BSQ 2008	0	0								
HY Male ODL 2007	2	15	25.6	4.9	29.8	9.8	15.0	5.1	160.5	51.3
HY Male ODL 2008	0	0								

Appendix 2 notes

[1] Note: 3 individuals returned the second season; therefore the years sum to 42 rather than 39.
[2] Note: 2 AHY males returned the second season; therefore the years sum to 13 rather than 11.
[3] Note: 1 HY male returned as AHY male during second season; therefore counted as AHY male during second season, even though it was the same individual.