

NOCTURNAL FORAGING BEHAVIOR OF WINTERING SURF SCOTERS AND WHITE-WINGED SCOTERS

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Abstract. We studied the nocturnal foraging behavior of Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) during winter in coastal British Columbia, Canada. Using radio telemetry, we collected nocturnal and diurnal data documenting the frequency of foraging dives and the location of scoters in relation to their intertidal foraging grounds. We found that dive foraging rarely occurred during nocturnal periods for either species. Only 2% of nocturnal observation blocks for both scoter species contained diving, compared with 98% of diurnal observation blocks. This corresponded to an average of only 0.1 min spent underwater per half-hour observation block during the night and over 7 min during the day. Both species of scoters were located farther offshore and in deeper waters during nocturnal hours, indicating that they were not using intertidal foraging areas at night. Our results suggest that Surf Scoters and White-winged Scoters face daylight-imposed limits on the amount of available foraging time. These potential day-length restrictions should be considered when reviewing human activities that potentially alter the amount of available foraging time or food supplies in winter habitats.

Key words: diving, *Melanitta perspicillata*, *Melanitta fusca*, nocturnal foraging, Surf Scoter, White-winged Scoter, winter.

Comportamiento de Forrajeo Nocturno de *Melanitta perspicillata* y *M. fusca*

Resumen. Se estudió el comportamiento de forrajeo nocturno de *Melanitta perspicillata* y *M. fusca* durante el invierno en la costa de British Columbia. Utilizando radio-telemetría, se colectaron datos nocturnos y diurnos sobre la frecuencia de buceos para alimentarse y la ubicación de las aves con relación a la zona intermareal. Se encontró que los buceos nocturnos son infrecuentes para ambas especies. Sólo en el 2% de las observaciones nocturnas de ambas especies se presentaron instancias de buceo, en comparación con el 98% de las observaciones diurnas. Esto corresponde a un promedio de 0.11 minutos bajo el agua por cada 30 minutos de observación durante la noche y más de 7 minutos durante el día. Ambas especies se ubicaron más alejadas de la costa y en aguas más profundas durante la noche, indicando que los individuos no utilizaron zonas intermareales durante este periodo. Estos resultados sugieren que *M. perspicillata* y *M. fusca* enfrentan restricciones en el número de horas disponibles para alimentarse en función de la cantidad de luz. El efecto de la duración del día debe ser considerado cuando se estudia el impacto de actividades humanas que pueden alterar el tiempo disponible para forrajeo o la cantidad de alimento durante el invierno.

INTRODUCTION

Understanding the foraging strategies that animals employ when balancing energy budgets can lead to a clearer understanding of potential constraints to populations, as well as species' behavioral scope when responding to environmental change (Pyke 1984). The allocation of time to foraging varies among taxa and individuals,

and can have important implications for meeting energy requirements (Bautista et al. 1998). When faced with food or energetic shortfalls, the ability to adjust foraging time allows animals to maintain the necessary rate of energy acquisition. For obligate diurnal foragers, day length imposes strict limits on available foraging time. However, having the flexibility to forage both diurnally and nocturnally greatly increases the amount of potential foraging time.

Studies have shown that some waterfowl regularly forage at night (Owen 1990, McNeil et al.

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1992), while others extend foraging into nocturnal periods when food is scarce or day length is short (Lane and Hassall 1996, Systad and Bustnes 2001). Most sea duck species (tribe Mergini) are thought to be diurnal foragers (Nilsson 1970, Guillemette et al. 1992, McNeil et al. 1992), although few data exist to adequately address this assumption. This information gap limits thorough understanding of sea duck foraging ecology and energetics.

Many sea duck species winter at northern temperate to subarctic latitudes, where day length is short and ambient temperatures are low during mid-winter. This combination of winter conditions, which reduces diurnal foraging time and increases energy demands, may require that sea ducks forage at night to obtain necessary energy requirements. Previous studies have shown that some sea duck species compensate for short winter days by increasing the proportion of daylight hours spent feeding (Guillemette 1998, Fischer and Griffin 2000, Systad et al. 2000) or by extending their feeding into low-light crepuscular periods (Nilsson 1970, Systad et al. 2000). However, recent data from high latitudes have demonstrated nocturnal feeding by some sea duck species during the shortest days of winter (Systad and Bustnes 2001). These nocturnal foraging sea ducks fed in shallow waters and employed non-dive feeding behaviors, such as surface-feeding and up-ending (Systad and Bustnes 2001). Owing to the high energetic cost of diving (de Leeuw 1996), the utilization of shallow water habitats and surface-feeding techniques may minimize energetic foraging costs that may be higher during nocturnal hours.

Surf Scoters (*Melanitta fusca*) and White-winged Scoters (*Melanitta perspicillata*) are believed to feed only diurnally (McNeil et al. 1992), although no studies have attempted to directly measure their nocturnal foraging during winter. Both scoter species feed primarily on bivalves during winter (Bourne 1984, Vermeer and Bourne 1984). Bivalves are sessile and often concealed beneath the substrate, potentially minimizing the need for visually directed predation. Indeed, some non-sea duck species of diving ducks (tribe Aythyini) commonly prey upon bivalves at night (Nilsson 1970, Pedroli 1982, Custer et al. 1996). Therefore, scoters could potentially utilize nocturnal foraging, especially under conditions of shortened day length, de-

creased food availability, or diurnal anthropogenic disturbances.

To determine the extent to which Surf Scoters and White-winged Scoters forage nocturnally, we monitored their nocturnal activities in Baynes Sound, British Columbia, Canada during the winters of 2002–2003 and 2003–2004. The paucity of information about nocturnal foraging by sea ducks is largely due to the difficulty of locating and observing them at night. To overcome these difficulties, we used radio-telemetry to remotely monitor the location and diving behavior of scoters during the nocturnal period. Our objective was to gain an understanding of nocturnal foraging behaviors of scoters by determining (1) the frequency of foraging dives at night, and (2) the location of scoters at night in relation to their intertidal foraging grounds. While documentation of diving provides a definitive quantification of nocturnal foraging, location data also provide information regarding the potential use of nondive-foraging behaviors in shallow water habitats. These nocturnal data were compared with similarly collected diurnal data to provide an understanding of scoter foraging activity over a 24-hour period.

METHODS

STUDY AREA

Our study area is located in the Strait of Georgia on the east coast of Vancouver Island, British Columbia, Canada, and encompasses the marine waters of Baynes Sound (49.5°N, 124.8°W). Baynes Sound is a 40-km long coastal channel fringed by a number of small, protected bays. Large expanses of gravel and sand sediments compose a majority of the intertidal habitat in Baynes Sound (Dawe et al. 1998). The area produces significant amounts of both wild and cultured bivalves, and is internationally recognized as an important wintering area for populations of waterfowl and other marine birds (Dawe et al. 1998). Of the diving duck species, Surf Scoters and White-winged Scoters are most numerous, accounting for 41% of all diving ducks in Baynes Sound (Dawe et al. 1998). Waterbird surveys in Baynes Sound for the winters of 2002–2003 and 2003–2004 estimated a mean population (\pm SE) of ca. 6500 \pm 250 scoters (Surf Scoters and White-winged Scoters). Surf Scoters and White-winged Scoters within Baynes Sound feed almost exclusively on infaun-

nal bivalves (clams) in small sediment, intertidal areas (Canadian Wildlife Service [CWS], unpubl. data).

SCOTER CAPTURES

Surf and White-winged Scoters were captured during December 2002 and 2003 using modified floating mist nets (Kaiser et al. 1995). Mist nets were deployed predawn and positioned in foraging areas used by scoters. Captured scoters were removed from mist nets, placed into holding kennels, and transferred to shore for radio-transmitter implantation. Radio transmitters with external antennae were surgically implanted in the abdominal cavities of Surf Scoters (2002: 27 males, 15 females; 2003: 18 males, 9 females) and White-winged Scoters (2002: 21 males, 13 females; 2003: 28 males, 20 females). Abdominally implanted transmitters have been successfully used in other sea duck species without evidence of either short-term (Mulcahy and Esler 1999) or long-term (Esler et al. 2000) consequences. The transmitters (Holohil Systems, Ltd., Carp, Ontario) were cylindrical, weighed 17.5 g, transmitted at 45 pulses per minute, and contained mortality switches that doubled the pulse rate if the transmitter remained motionless for ≥ 12 hr. Surgeries to implant radio transmitters were performed by experienced veterinarians following procedures developed for other sea duck species (Mulcahy and Esler 1999). Scoters were held for at least one hour postsurgery and subsequently released at their capture sites.

RADIO TELEMETRY

We monitored the diving behavior and locations of radio-marked scoters during the winters of 2002–2003 (20 December–15 March) and 2003–2004 (1 November–1 March). Diving behavior data were gathered only during the winter of 2002–2003. Collection of location data in 2003 began in November, prior to that winter's transmitter deployment, due to the return of radio-marked scoters from the previous winter. We concluded monitoring each winter at the start of herring spawning, at which point scoters abandoned their typical winter habitats and food sources within Baynes Sound.

Dive behaviors of radio-marked scoters were monitored with hand-held 4-element Yagi antennas connected to Advanced Telemetry Systems (ATS; Isanti, Minnesota) R4000 receivers. The

radio signal disappeared when the bird dove and resumed when the bird resurfaced, allowing the observer to document both the occurrence and duration of foraging dives (Wanless and Harris 1991, Custer et al. 1996). To determine the appropriate observation duration, radio signals were monitored diurnally for ≥ 1 hr. Of all diurnal nondiving periods lasting ≥ 5 min ($n = 1320$), only 4.5% were ≥ 30 min. Therefore, a 30-min observation time was used for monitoring, given the high likelihood of detecting dive foraging if it were to occur. The number of dives and length of each individual dive (± 1 sec) were recorded during each 30-min observation block. Telemetry observations were conducted diurnally and nocturnally at multiple sites throughout Baynes Sound that offered both unobstructed water views and heightened elevation. Nautical twilight was used to define the boundary between night and day, as it assured almost complete darkness for nocturnally defined time periods. Start times of telemetry observation bouts were set so that a broad range of tide levels were frequently and evenly sampled within both diurnal and nocturnal periods. Furthermore, sampling bouts within nocturnal and diurnal observation periods were evenly spread across winter dates and the 24-hr cycle. Daytime visual observations of radio-marked scoters were used to confirm the loss of radio-signal during a dive. These observations also confirmed that scoters foraged exclusively by diving during the day, not engaging in surface feeding behaviors that might not result in radio signal loss.

Point locations of radio-marked scoters were determined using triangulation with vehicles outfitted with two 4-element Yagi antennas mounted on extending masts (White and Garrott 1990). Yagi antennas were connected to ATS R4000 receivers and equipped with null and peak combiners. Compass bearings for each radio-marked individual of interest were collected simultaneously by two different observers at known telemetry locations, eliminating location error associated with animal movement (Schmutz and White 1990). Diurnal point locations were collected at least once per week for each radio-marked individual within the study area. Nocturnal locations were collected less frequently, with approximately one point location obtained monthly per individual within the study area. Telemetry accuracy tests of point locations indicated that signal bearings collected by observers

had a standard deviation of $\pm 4.2^\circ$ from the true bearing. Using this standard deviation, the mean (\pm SE) 90% error polygon for all nocturnal and diurnal bearings was estimated to be 3.0 ± 0.2 ha (Lee et al. 1985, White and Garrott 1990), a sufficient accuracy for our point-location analyses.

We estimated point-location coordinates and distances between the observer and point locations using Location of a Signal (LOAS v.3.0) triangulation software (Ecological Software Systems, Ltd., Sacramento, California). Location data were filtered to assure we were using the most accurate information, excluding locations that met the following criteria: locations with nonintersecting bearings, locations without bearing separation between 20° and 160° , locations estimated to be on land, and locations with observer to location distances ≥ 4 km. Locations ≥ 4 km from the observer were unreliable due to weak radio-signal reception. Only one location per individual during a single diurnal or nocturnal observation session was used in the analyses. If more than one location per individual was obtained during an observation session, a single location was randomly selected for inclusion in analyses.

We used ArcView v.3.2 (ESRI 1999) geographic information system (GIS) software and associated supplementary extensions to retrieve geographic characteristics of points representing scoter locations. To determine the minimum distance between each point location and shore, we plotted point locations on a digital 1:20 000 TRIM base-map of the British Columbia coast (British Columbia Ministry of Sustainable Resource Management). The TRIM base-map shoreline within our study area was divided into 10-m segments using the Polyline-Chopper script (Gee 2004) developed for ArcView v.3.2. The distance was then estimated using the Nearest Features v.3.7a extension (Jenness 2004), which measured the distance between the point location and the center of the nearest 10-m shoreline segment. Water depth at point locations was determined by intersecting the point locations with a digitized 1:40 000 Baynes Sound nautical bathymetry chart (Fisheries and Oceans Canada, no. 3527) using the Geoprocessing extension built into ArcView v.3.2. Depth zones were defined as either intertidal or subtidal, with subtidal waters being broken into 10-m depth zones (i.e., 1–10 m, 11–20 m, etc.).

Intertidal zone includes all locations where depth ≤ 0 m at the lowest low tide. For statistical analyses, intertidal locations were scored as 0-m depth and the midpoint of each subtidal 10-m depth zone was used for all other depths.

STATISTICAL ANALYSES

We estimated the frequency of dive foraging for diurnal and nocturnal periods as the proportion of 30-min observation blocks containing ≥ 1 dive. The amount of time spent foraging was determined by summing the total amount of time spent underwater per 30-min observation block. Time spent foraging and frequencies of dive foraging were compared between diurnal and nocturnal periods.

We used an information-theoretic approach for data analysis (Burnham and Anderson 2002). We examined three response variables: (1) total time underwater per 30 min (2) water depth, and (3) distance to shore. For each response variable, we fit a series of candidate general linear mixed models (Littell et al. 2000) using PROC MIXED of program SAS (SAS Institute 1999). The candidate model set for each response variable incorporated the same explanatory variables: species (Surf Scoter, White-winged Scoter), sex, and night/day (defined nominally as either night or day). Without any background knowledge of scoter nocturnal behavior or species and sex differences, all additive model combinations of the explanatory variables and all single explanatory variable models were regarded as biologically plausible. A null model was also included in each candidate model set to assess model fit (Burnham and Anderson 2002). Models with interaction terms were not used in order to restrict the number of candidate models and because there were no strong biological explanations for putative interactions. Thus, identical candidate model sets for each response variable consisted of all single explanatory variable models, all additive combination models, and a null model. We used Akaike's Information Criterion (AIC) to rank the fit of each model within a candidate set (Burnham and Anderson 2002). For each of our analyses, the large sample size (n) relative to the total number of parameters (k) did not require the use of small-sample-size AIC corrections. Δ AIC were used to compare the relative explanatory value of the candidate models, with Δ AIC defined as the difference between the AIC value of the best-fitting model and each respec-

TABLE 1. Minutes diving per 30-min observation block and distance to shore (m) of Surf Scoters and White-winged Scoters wintering in coastal British Columbia, 2002–2004. Data are summarized for day and night periods, and scoter species. Values are presented as means \pm SE and numbers in parentheses indicate sample sizes.

	Surf Scoter		White-winged Scoter	
	Minutes diving per 30 min	Distance to shore (m)	Minutes diving per 30 min	Distance to shore (m)
Day	7.2 \pm 0.3 (271)	231.1 \pm 8.4 (481)	6.9 \pm 0.2 (316)	254.4 \pm 9.6 (649)
Night	0.1 \pm 0.1 (61)	703.8 \pm 44.0 (46)	0.2 \pm 0.1 (77)	911.6 \pm 54.1 (58)

tive model in the set. Thus, $\Delta\text{AIC} = 0$ for the model of best fit. All models with a $\Delta\text{AIC} \leq 2$ were considered to have substantial support and received consideration in making data inferences (Burnham and Anderson 2002). AIC weights (w_i), which indicate the relative likelihood of a model given the data and set of candidate models, also were calculated to provide a relative weight of evidence for each model (Burnham and Anderson 2002). To determine the relative importance of each explanatory variable within a candidate model set, AIC weights were summed for all candidate models containing the explanatory variable under consideration, providing a parameter likelihood value. Also, weighted parameter estimates and unconditional standard errors were calculated for the explanatory variables in each analysis, based on AIC weights for all candidate models, to account for model uncertainty (Burnham and Anderson 2002).

General linear mixed models were used to account for repeated measures on radio-marked individuals and to include subject as a random effect (Littell et al. 2000). Mixed models structure the correlation of residuals both within and among individuals by incorporating covariance parameters in the models. The covariance structures we considered for each response variable included the spatial power law, both with and without a random between-subject effect, to model decreasing correlation with increasing time between repeated observations and compound symmetry to model constant correlation among repeated observations. The best-fitting covariance structure for each response variable was chosen using AIC model selection criteria (Littell et al. 2000). For the response variables of distance to shore and water depth, compound symmetry was selected as the best fitting covariance structure. For total time underwater per

30 min, the spatial power law structure with a random between-subject effect was chosen as the best-fitting covariance structure. The selected covariance structure for each response variable was included in all fixed effects candidate model combinations.

RESULTS

DIVE FORAGING

Of 587 diurnal 30-min observation blocks for both Surf Scoters and White-winged Scoters combined, 98% of observation blocks contained radio-signal loss indicative of diving. In contrast, only 2% of 138 nocturnal observation blocks contained diving. Results were similar for both species, as Surf Scoters dove in 97% of diurnal observations ($n = 271$) and 3% of nocturnal observations ($n = 61$), and White-winged Scoters dove during 98% of diurnal observations ($n = 316$) and 1% of nocturnal observations ($n = 77$).

Both scoter species spent more time diving during the day than at night (Table 1). Results indicated that the model containing only night/day as an explanatory variable best explained variation in minutes diving per 30 min (Table 2). Two additional model combinations also received substantial support ($\Delta\text{AIC} \leq 2$), each of which included night/day (Table 2). All models without night/day received no empirical support from the data ($\Delta\text{AIC} > 265$, $w_i = 0$). Further, only night/day had a large parameter likelihood value and 95% confidence intervals (weighted parameter estimate $\pm 1.96 \times \text{SE}$) that did not overlap zero (Table 3). Hence, species and sex offered little value for explaining variation in the amount of time spent diving.

WATER DEPTH

In general, both scoter species were located within intertidal areas during diurnal hours and

TABLE 2. General linear mixed models evaluating variation in foraging effort and location of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2002–2004. Night/day is a categorical variable with two levels (night and day). For all models, the number of parameters (k) includes $+1k$ for an intercept and $+1k$ for variance estimate. Covariance structures for repeated measures and random between-subject effect include $+2k$ for all models of minutes diving per 30-min observation block and $+1k$ for all models of water depth and distance to shore. Only models with $w_i > 0.01$ and the null model are presented. Candidate models are listed in order of ΔAIC .

Response variable	Model	k	Log-likelihood	ΔAIC	AIC weight (w_i)
Minutes diving per 30 min	night/day	5	-1907.06	0.00	0.46
	night/day + species	6	-1906.88	1.26	0.25
	night/day + sex	6	-1907.11	1.74	0.19
	night/day + species + sex	7	-1906.74	3.03	0.10
	null	2	-2095.10	369.71	0.00
Water depth (m)	night/day	4	-4627.61	0.00	0.41
	night/day + species	5	-4627.17	1.14	0.23
	night/day + sex	5	-4627.19	1.19	0.23
	night/day + species + sex	6	-4626.74	2.31	0.13
	null	2	-4784.30	309.40	0.00
Distance to shore (m)	night/day + species	5	-8277.47	0.00	0.63
	night/day + species + sex	6	-8277.45	1.96	0.24
	night/day	4	-8280.34	6.39	0.10
	night/day + sex	5	-8280.31	16.97	0.03
	null	2	-8536.70	512.43	0.00

in subtidal areas during nocturnal hours (Fig. 1). The model that best explained variation in water depth at scoter locations contained only night/day as an explanatory variable (Table 2). The model containing night/day and species, as well as the global model, also received substantial support ($\Delta AIC \leq 2$), although their AIC weights

were low ($w_i = 0.23$) relative to the top model ($w_i = 0.41$). Model combinations not including night/day as an explanatory variable received no empirical support, as indicated by their large ΔAIC values ($\Delta AIC > 289$) and low AIC weights ($w_i = 0$). Parameter likelihoods and parameter estimates further emphasized the impor-

TABLE 3. Parameter likelihoods and weighted parameter estimates \pm unconditional SE from general linear mixed models evaluating variance in foraging effort and location of radio-marked Surf Scoters and White-winged Scoters during winter in coastal British Columbia, 2002–2004. Explanatory variables are listed in order of parameter likelihood values. Parameter likelihoods are the summed AIC weights (w_i) for all candidate models containing the explanatory variable under consideration.

Response variable	Explanatory variable	Parameter likelihood	Parameter estimate \pm SE
Minutes diving per 30 min	Intercept		0.11 \pm 0.40
	Night/day ^a	1.00	6.77 \pm 0.37
	Species ^b	0.35	0.14 \pm 0.18
	Sex ^c	0.29	-0.07 \pm 0.15
Water depth (m)	Intercept		26.07 \pm 1.25
	Night/day ^a	1.00	-21.39 \pm 1.18
	Species ^b	0.36	0.34 \pm 0.42
	Sex ^c	0.36	0.34 \pm 0.43
Distance to shore (m)	Intercept		854.01 \pm 27.15
	Night/day ^a	1.00	-584.07 \pm 20.65
	Species ^b	0.87	-47.54 \pm 20.65
	Sex ^c	0.27	1.49 \pm 6.29

^a Night/day is a categorical variable (day or night) with night as the reference value.
^b Species is a categorical variable (Surf Scoter or White-winged Scoter) with White-winged Scoter as the reference value.
^c Sex is a categorical variable (male or female) with male as the reference value.

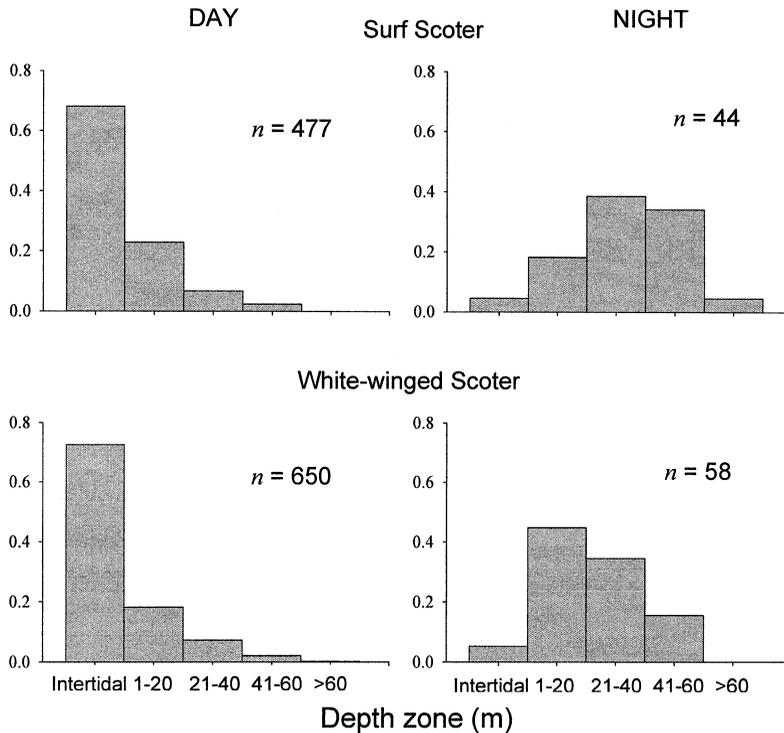


FIGURE 1. Proportion of telemetry point locations by water depth zone for wintering Surf Scoters and White-winged Scoters during day and night periods in coastal British Columbia, 2002–2004. Intertidal zone includes all locations where depth ≤ 0 m at the lowest low tide. All other locations are grouped into 20-m depth zones.

tance of night/day as an explanatory variable (Table 3). Night/day had a parameter likelihood = 1.00, indicating that only models containing night/day were well supported. Parameter likelihood values for species and sex were much lower than night/day and their parameter estimates had relatively large unconditional SE (Table 3).

DISTANCE FROM SHORE

Both scoter species were located closer to shore during day than at night (Table 1). The best-fitting candidate model included night/day and species as explanatory variables (Table 2). The next best-fitting model, with a $\Delta\text{AIC} \leq 2$, was the global model containing night/day, species, and sex as explanatory variables. All models without night/day received no support, as indicated by their large ΔAIC values (>468) and low AIC weights ($w_i = 0$). Night/day had a parameter likelihood = 1.00 and the unconditional SE was small relative to the weighted parameter estimate, indicating that night/day had strong explanatory value for variation in distance to shore

(Table 3). The species parameter also was well supported, with a parameter likelihood = 0.87, and the parameter estimate indicating that Surf Scoters tended to be closer to shore than White-winged Scoters (Table 3). The sex parameter was not well supported, as indicated by a small parameter likelihood value and a unconditional SE that is larger in magnitude than the actual parameter estimate.

DISCUSSION

We found dramatic differences in foraging behaviors of Surf Scoters and White-winged Scoters between diurnal and nocturnal periods. Our results indicated that Surf Scoters and White-winged Scoters rarely forage at night. Only 2% of nocturnal observation blocks contained radio-signal loss indicative of diving, compared to 98% of diurnal observation blocks. This corresponded to an average of only 7 sec of diving per 30 min during nocturnal periods, compared to over 7 min during daylight hours. Information theoretic analyses of model sets indicated that amount of time spent diving was almost wholly

explained by day or night period, with little effect associated with species or sex.

Both species of scoters were located farther offshore and in deeper waters during nocturnal hours, generally removed from the intertidal foraging areas used during the day. The concomitant relationship between distance from shore and water depth was expected, given that these variables are highly positively correlated. Mean distances to shore for Surf Scoters and White-winged Scoters were 231 m and 254 m during the day, respectively, compared to 704 m and 911 m during the night. Likewise, 70% of diurnal locations of both scoter species were within the intertidal area, compared with only 5% of nocturnal locations. Other sea duck species have been documented utilizing nondive foraging behaviors during nocturnal hours, such as surface feeding or up-ending during low tides (Systad and Bustnes 2001). For sea-duck species that prey upon infaunal or epifaunal invertebrates, such nondive-foraging behaviors would require shallow water to access prey items from the surface. These nondive-feeding behaviors, which were never diurnally witnessed for scoters, do not result in a lost radio-signal and would thus not be detected by our radio-telemetry observations. The deep water, offshore location of scoters during nocturnal hours, however, precludes the potential use of nondive-feeding behaviors. This result further indicates that the observed differences between day and night foraging behaviors reflect true differences in foraging effort.

Of the three individual scoters detected foraging at night, one was detected on 17 January and two were detected on 22 January. The duration of daylight on these days was approximately 10 hr, which is only 35 min longer than the shortest day of the year. The rare occurrence of nocturnal diving during the shortest days of winter suggests that these scoters may have been compensating for the short duration of daylight. No further nocturnal diving was detected despite continued monitoring until mid-March. During the shortest days of winter, some sea duck species extend their diurnal feeding into low-light crepuscular periods to cope with reduced daylight (Systad et al. 2000). With regards to sunrise and sunset, the scoter on the 17 January was diving 2 hr before sunrise and the two scoters on the 22 January were diving approximately 4 hr after sunset. None of these nocturnal foraging

bouts were adjacent to daylight periods, indicating that these scoters were not merely extending their diurnal diving into periods adjacent to sunrise and sunset, but rather were actively choosing to engage in nocturnal foraging.

The low rate of nocturnal foraging by scoters can be broadly explained by two exclusive hypotheses: (1) scoters are unable to forage nocturnally, or (2) scoters choose not to forage nocturnally. An inability to forage nocturnally would result from a complete dependence upon visual cues for location of prey. The fact that we observed nocturnal foraging, albeit rarely, suggests that scoters possess this ability. Other diving ducks are known to forage on infaunal bivalves at night (Klima 1966, Nilsson 1970, Custer et al. 1996), presumably using tactile cues, suggesting that it would be possible for scoters. Therefore, it appears that scoters are choosing not to forage nocturnally. Nonprofitable nocturnal foraging, nocturnal predation risk, and visual constraints, acting solely or in combination, could potentially force scoters to avoid nocturnal foraging. Also, acquisition of sufficient energy quantities during daylight hours may preempt the need for nocturnal foraging. Below, we consider potential reasons scoters at our study site rarely foraged at night.

Scoters in Baynes Sound feed primarily on clams, which are abundant throughout much of the intertidal zone (Bourne 1984, Vermeer and Bourne 1984). Clams within Baynes Sound may be so abundant and energetically profitable that the daily energetic requirements of scoters can be sufficiently met during daylight hours, making nocturnal foraging unnecessary. Other wintering areas with different prey items and abundances could alter a scoter's decision to forage nocturnally.

At the latitude of our study area (49°N), the amount of daylight within our study site ranges between 9 and 10 hr during the shortest days of winter. Nocturnal hours thus predominate the 24-hour cycle during winter, a potentially significant amount of time from which to abstain from foraging. Along the Pacific coast, Surf Scoters and White-winged Scoters winter as far north as coastal Alaska (60°N), experiencing less than 7 hr of daylight during midwinter (Brown and Fredrickson 1997, Savard et al. 1998). Nocturnal foraging studies of other sea duck species have been conducted at high northern latitudes. Systad and Bustnes (2001) documented noctur-

nal foraging and increased crepuscular foraging by Steller's Eiders (*Polysticta stelleri*) during the shortest days of winter at the northern extent of their wintering range (70°N). However, Rizzolo et al. (2005) found that Harlequin Ducks (*Histrionicus histrionicus*) wintering at 60°N did not forage at night. Although scoters within our study site rarely engaged in nocturnal foraging, this foraging strategy may be necessary at more northerly latitudes to compensate for the shortened day length. Scoters residing at the southern extent of their winter range, including the coastal waters of California and Baja California, clearly have greater time-budget flexibility and may not need to forage nocturnally as a result of day-length constraints.

Among diving ducks, some non-sea duck species (tribe Aythyini) commonly feed both diurnally and nocturnally on infaunal invertebrates, presumably locating prey using tactile methods (Klima 1966, Nilsson 1970, Custer et al. 1996). The regularity of this behavior indicates that these diving duck species can profitably dive-forage at night without reliance upon visual cues. Additionally, some sea duck species are known to dive to depths greater than 40 m (Guillemette et al. 1993, Lovvorn et al. 2003), presumably foraging in very low light levels or complete darkness at such depths. Within our study area, scoters foraging during the day were diving almost exclusively in the intertidal zone (DE, unpubl. data), typically in water depths less than 5 m. Winter water clarity in our study area was high (>5 m) due to the reduced plankton load, and benthic organisms were well lit during daylight hours at shallow water depths (TLL, pers. obs.), likely providing scoters full visual acuity. During night, however, the loss of visual cues and greater dependence upon tactile cues may make nocturnal foraging energetically unprofitable and thus avoided by scoters. Potential visual cues for scoters foraging on clams may include the location of clam siphon holes or the recognition of successful bivalve capture by other foraging scoters, indicating profitable feeding patches. Indeed, scoters almost always feed in groups (Beauchamp 1992, Savard et al. 1998) and underwater group feeding dynamics, such as recognition of successful prey capture by conspecifics or group digging, seems highly plausible.

The offshore location of scoters at night may be a predator avoidance tactic. Predation risk

near shore at night, from nocturnally active predators such as mink (*Mustela vison*) or river otters (*Lutra canadensis*), may offset any energetic advantages gained from foraging nocturnally. During the day, scoters can visually assess predation risk from common predators such as Bald Eagles (*Haliaeetus leucocephalus*), providing sufficient warning to reduce predation risks. Without the aid of visual predator recognition, scoters may be susceptible to near-shore predation pressures and thus move to safer, offshore waters at night.

Future studies are needed across a range of latitudes, habitats, and food availabilities to fully understand the nocturnal behaviors of scoters. Further, a histological examination of the eyes of sea ducks, including rod and cone counts, could provide an indication of the ability of sea ducks to feed in darkness. The overall rarity of nocturnal foraging in our study site, however, strongly suggests that the amount of foraging time available to Surf Scoters and White-winged Scoters may be daylight limited, a potentially important restriction considering the northern winter ranges of both species. This restriction may limit the ability of scoters to increase time spent foraging in response to potential food or energetic shortfalls. Daylight restrictions could be especially limiting during the shortest days of winter and at high northerly wintering latitudes. Anthropogenic disturbances, such as hunting, have been known to force some waterfowl species to adjust their daily activity patterns and increase nocturnal foraging in response to the loss of diurnal foraging time (Raveling et al. 1972, McNeil et al. 1992). Although lightly hunted along the Pacific coast during winter, similar disturbances from industrial, nautical, or other anthropogenic activities could restrict daytime foraging opportunities for scoters. Decreases in available food supplies could exert similar foraging-time pressures, forcing individuals to spend more time searching for food while consuming less food per unit effort (Percival and Evans 1997, Tuckwell and Nol 1997). The potential nocturnal foraging limitations of scoters should be considered when reviewing anthropogenic activities that may alter the amount of available feeding time or food supplies.

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