

# Foraging effort of Surf Scoters (*Melanitta perspicillata*) wintering in a spatially and temporally variable prey landscape

Molly K. Kirk, Daniel Esler, and W. Sean Boyd

**Abstract:** We monitored foraging effort of radio-tagged Surf Scoters (*Melanitta perspicillata* (L., 1758)) in three different habitats: (1) shellfish farm structures with high densities of mussels and strong seasonal prey depletion, (2) soft-bottom clam beds with more stable but less available prey, and (3) rocky intertidal beds with moderate mussel densities and depletion rates. We predicted that foraging effort would vary uniquely by habitat, with effort increasing more where depletion was strongest. However, variation in both hourly and daily foraging efforts was best explained by date only. Effort per hour was lowest in early December (presumably owing to very high prey abundance), increased until mid-February as prey declined, and then decreased again in March (probably owing to increased daylight time for foraging). Foraging effort estimated over a full day increased steadily from December to March as prey were depleted. Temporal patterns of effort did not vary by habitat after accounting for seasonal effects. Instead of increasing foraging effort in habitats with strong depletion, Surf Scoters redistributed to habitats with lower degrees of prey reduction as the season progressed. We suggest that Surf Scoters respond to variation in prey by adjusting both foraging effort and habitat selection as the prey landscape changes.

**Résumé :** Nous avons suivi les efforts de recherche de nourriture de macreuses à front blanc (*Melanitta perspicillata* (L., 1758)) munies d'une étiquette radio dans trois habitats différents : (1) des structures d'élevage de coquillages avec de fortes densités de moules et une importante déprédation saisonnière, (2) des lits de palourdes à fond meuble avec des proies plus stables mais moins disponibles et (3) des fonds intertidaux rocheux avec des densités moyennes de moules et des taux de déprédation modérés. Nous avons prédit que les efforts de recherche de nourriture varieraient de façon particulière dans chaque habitat et que l'effort augmenterait plus là où la déprédation est la plus importante. Cependant, les variations horaires et journalières de l'effort de recherche de nourriture s'expliquent le mieux par la seule date. L'effort par heure est minimal en décembre (ce qui est sans doute dû à une tre



morning before dawn, floating sets of nets and decoys were placed at Surf Scoter foraging sites. As birds were captured, they were placed in kennels and transported to a banding station where they were banded and weighed; sex was determined by plumage characteristics (Iverson et al. 2003) and age class was estimated by bursal probing (Mather and Esler 1999). Either subcutaneous or internal abdominal VHF radios with external antennae were then implanted in Surf Scoters ( $n = 74$ ), following standard procedures (Mulcahy and Esler 1999). These radio types have been shown to perform well for Surf Scoters, with low mortality rates and good signal strength and accuracy for telemetry (Iverson et al. 2006). All capture, banding, and radio-implantation procedures were approved by the Animal Care Review Committee at Simon Fraser University.

The radio signal of VHF transmitters disappears when the bird submerges and resumes upon resurfacing (Custer et al. 1996), allowing quantification of time spent foraging by diving birds. Following methods of Lewis et al. (2005, 2008), radio-tagged Surf Scoters were monitored for 1 h periods at selected foraging locations covering all three habitat types (clam flats, farms, and intertidal mussel beds) over the season. The 1 h observation periods spanned available daylight hours throughout the season, ranging from 0800 to 1700. A hand-held four-element Yagi antenna was positioned for optimal signal strength from a land-based observation point and connected to a radio receiver (Advanced Telemetry Systems, Isanti, Minnesota). During the 1 h observation period, each dive length was recorded as minutes underwater measured to the nearest second using a standard stopwatch. Individuals were monitored a maximum of once per day. At the end of the observation period, the total minutes underwater per hour were summed. For each individual 1 h observation, daily foraging time, or total minutes underwater per day, was also estimated. Because Surf Scoters are generally diup4u

**Table 1.** General linear model selection results assessing variation in hourly (min underwater-h<sup>-1</sup>) and daily (estimated min underwater-d<sup>-1</sup>) foraging efforts of radio-tagged Surf Scoters (*Melanitta perspicillata*) in the Malaspina Inlet, British Columbia.

Response variable	Model	No. of parameters	$\Delta AIC_c$	AIC <sub>c</sub> weight
Hourly foraging effort	Date <sup>a</sup>	5	0.00	0.45
	Habitat + date	7	1.84	0.18
	Habitat + date + indiv <sup>b</sup>	9	2.54	0.13
	Date + envir <sup>c</sup>	8	4.26	0.05
	Date + habitat × date	9	4.62	0.05
	Habitat	5	4.89	0.04
	Indiv+ habitat × date	11	5.69	0.03
	Date + indiv + envir	10	5.91	0.02
	Habitat + date + indiv + envir	12	7.08	0.01
	Habitat + date + habitat × date	11	7.70	0.01
	Indiv	5	8.14	0.01
	Date + envir + habitat × date	12	8.37	0.01
	Habitat + date + indiv + habitat × date	13	8.85	0.01
	Habitat + envir	8	9.84	0.00
	Date + indiv + envir + habitat × date	14	10.22	0.00
	Habitat + date + envir + habitat × date	14	11.79	0.00
	Null	2	15.82	0.00
Daily foraging effort	Date	5	0.00	0.40
	Habitat + date + indiv	9	1.50	0.19
	Habitat + date	7	1.70	0.17
	Date + habitat × date	9	3.70	0.06
	Indiv + habitat × date	11	3.90	0.06
	Date + envir	8	4.60	0.04
	Date + indiv + envir	10	5.20	0.03
	Habitat + date + indiv + envir	12	6.50	0.02
	Date + envir + habitat × date	12	7.70	0.01
	Habitat + date + habitat × date	11	7.80	0.01
	Habitat + date + indiv + habitat × date	13	8.10	0.01
	Date + indiv + envir + habitat × date	14	8.80	0.00
	Habitat + date + envir + habitat × date	14	12.20	0.00
	Habitat	5	13.80	0.00
	Habitat + envir	8	18.00	0.00
	Indiv	5	21.60	0.00
	Null	2	35.80	0.00

**Note:** The number of parameters includes +1 for an intercept and +1 for a model variance estimated. Covariance structures for repeated measures include +1 parameter for all models except the null model. Models listed in order of  $\Delta AIC_c$ , where  $\Delta AIC_c$  is Akaike's information criterion adjusted for small sample sizes.

<sup>a</sup>Date = day + day<sup>2</sup>, where day 1 = 09 December 2004.

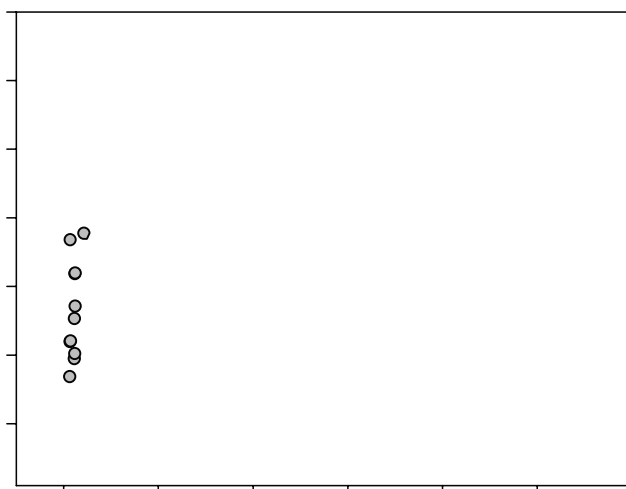
<sup>b</sup>Indiv = sex (male or female) + age (adult or hatch-year).

<sup>c</sup>

We used general linear mixed models generated from PROC MIXED in SAS version 9.1 (SAS Institute Inc. 2003), with a repeated-measures term to account for multiple observations on individual Surf Scoters. The use of mixed models allowed us to include subject as a random effect, thereby accounting for within-subject correlation (Littell et al. 2000). The structure of this correlation was incorporated as a covariance parameter in each model. Several covariance structures were considered by applying them to the global model (not including interaction terms) and AIC model selection criteria were used to select the best fitting structure. Compound symmetry covariance was deemed most appropriate to apply in the analysis. With a compound symmetry structure, the correlation between subjects is con-

stant regardless of the distance in time between pairs of observations (Littell et al. 2000).

An information-theoretic approach was used to evaluate fit of the candidate set of models (Burnham and Anderson 2002). Akaike's information criterion adjusted for small sample sizes (AIC<sub>c</sub>) was generated for each candidate model. The candidate set was ranked by  $\Delta AIC_c$ , the difference between the AIC<sub>c</sub> of the best fitting model and each model in the set. AIC<sub>c</sub> weights were used to deduce the relative support for each model. Also, parameter likelihood values were generated by summing the AIC<sub>c</sub> weights for all candidate models containing the parameter under consideration. These parameter likelihoods allow us to assess the relative importance of each variable within the model set; a



value close to one indicates a well-supported or important variable. Weighted parameter estimates with 95% confidence intervals (CIs) also were produced for each explanatory variable (Burnham and Anderson 2002); they provide another measure of the importance of individual parameters for explaining variation in the response variable.

## Results

Throughout winter, Surf Scoters spent a mean of  $11.7 \text{ min}\cdot\text{h}^{-1}$ , or 19.5% of their time, underwater in a foraging dive. In our mixed model analysis of minutes underwater per hour, the model including only the date variables was the most parsimonious for explaining variation in hourly foraging time ( $\text{AIC}_c$  weight = 0.45; Table 1). Hourly time spent diving was lowest in early December ( $7.8 \text{ min}\cdot\text{h}^{-1}$  or 13%), increased to  $12.6 \text{ min}\cdot\text{h}^{-1}$  or 21% by mid-February, and declined again slightly by late March ( $10.8 \text{ min}\cdot\text{h}^{-1}$  or 18%) ( $r^2 = 0.06$ ; Fig. 2). The habitat + date model ( $\text{AIC}_c$  weight = 0.18) received some support (Table 1), which suggested that some variation in hourly dive investment was due to habitat type. However, because the habitat  $\times$  date interaction models were not supported ( $\text{AIC}_c$

weights  $< 0.05$ ), the temporal pattern of minutes underwater per hour was similar in all habitats. The habitat + date + indiv model was the third most parsimonious ( $\text{AIC}_c$  weight = 0.13), although it received less than one-third of the support of the date model. All other models, including the null and global models, were very poorly supported.

The parameter likelihood values also supported the date variables (day and day<sup>2</sup>) as the best explanatory variables for minutes underwater per hour (Table 2). Their weighted parameter estimates confirmed that hourly dive effort tended to increase until mid-winter (day = 0.15, 95% CI = 0.06) then decreased slightly (day<sup>2</sup> = -0.001, 95% CI = 0.0005). The habitat variables, with parameter likelihood values of 0.38, were second to the date variables in their explanatory value (Table 2), although this was not a strong level of support. Mean dive time per hour was slightly lower on farms ( $10.5 \text{ min}\cdot\text{h}^{-1}$  or 17.5%) than at intertidal clam beds ( $12.7 \text{ min}\cdot\text{h}^{-1}$  or 21.2%) and intertidal mussel reefs ( $13.4 \text{ min}\cdot\text{h}^{-1}$  or 22.3%). Similarly, model-averaged parameter estimates revealed that Surf Scoters foraging in farm habitats spent less time underwater per hour compared with those foraging in intertidal mussel and clam beds (Table 2), although the 95% CIs broadly overlapped zero. Therefore,

despite these trends in habitat variation, this result was not strongly supported. None of the other variables received support for explaining variation in minutes underwater per hour, with all parameter likelihoods  $\leq 0.21$  and 95% CIs broadly overlapping zero (Table 2).

For daily time foraging, or minutes underwater per day,

ducted in late February established that several of our radio-tagged Surf Scoters had moved to occupy foraging locations outside the study area.

## **Discussion**

We found that Surf Scoters wintering in Malaspina Inlet

habitat choice and movements. Alternatively, Surf Scoters may balance foraging effort with habitat selection to optimally meet their energetic requirements. Also, as hourly and daily foraging efforts increased in mid-winter (February), many Surf Scoters departed the study area to forage elsewhere (Fig. 4). These movements are too early in the year to be migratory (S. Wainwright De La Cruz, unpublished data). As the demands of feeding in an area with declining prey increased, clearly many birds sought alternative feeding areas.

Our study confirms that Surf Scoters adjust both foraging effort and habitat selection during the winter season. When faced with declining prey, Surf Scoters can increase foraging efforts to work harder or, alternatively, move to habitats with increased prey abundance. We found no evidence of habitat- or prey-specific foraging behaviours. Surf Scoters appear to respond to prey depletion in specific habitats by adjusting both levels of foraging effort and habitat or prey selection.

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