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HAUL-OUT SELECTION BY PACIFIC HARBOR SEALS (*PHOCA VITULINA RICHARDII*): ISOLATION AND PERCEIVED PREDATION RISK

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ABSTRACT

The potential for non-aquatic predators to influence habitat use by harbor seals (*Phoca vitulina*) in a nearshore marine environment was studied by examining haul-out site use and through an experimental approach. Distance from shore, distance to possible foraging depths, peripheral water depth, and haul-out areas were quantified for each haul-out. There was a positive relationship between the number of seals hauled out and the distance from shore for eight known haul-out sites. The hypothesis that harbor seals increasingly hauled out farther offshore to reduce predation risk was tested experimentally by measuring their response to a model of a potential terrestrial predator in comparison to a control object, and to disturbance by a human at one of the study sites. Harbor seals abandoned the haul-out in the presence of the predator model, but showed little response to the controls, suggesting they possess a threat image for terrestrial predators and avoid hauling out when it is perceived. These results support the hypothesis that harbor seals select isolated sites to reduce exposure to terrestrial carnivores.

Key words: habitat selection, predation risk, harbor seal, *Phoca vitulina,* field experiment, pinnipeds.

The selection of inaccessible coastal or offshore locations by seals when "hauling out" onto land, has been attributed to pressure from terrestrial predators (Stirling 1983, Da Silva and Terhune 1988, Riedman 1990). The lack of documented observations of terrestrial carnivores preying on harbor seals has led others to suggest that alternative hypotheses, such as increased mating potential where females aggregate at higher density (Renouf and Lawson 1986,

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Walker and Bowen 1993, Thompson *et al.* 1994, Van Parijs *et al.* 1997), or proximity to foraging grounds (Härkönen 1987) may explain site selection.

Although there are few direct observations of non-aquatic predators preying on harbor seals, this does not exclude the possibility that seals are avoiding the shoreline as a means of reducing their risk to potential terrestrial predators where their ranges overlap. In fact, the predator avoidance behavior may be so successful that it is difficult to observe the behavioral sensitivity of the prey species to the risk (Lima and Dill 1990). Indirect evidence for predator avoidance behavior in haul-out site selection by harbor seals has come from studies of site fidelity, where the repeated use of a limited number of haul-out sites has been postulated to be related to reliable food sources in areas with few or no natural predators (Pitcher and McAllister 1981, Brown and Mate 1983, Suryan and Harvey 1998). Harbor seals show pronounced avoidance behaviors near aquatic predators such as *transient* killer whales (*Orcinus orca*) (Stacey and Baird 1989, Ford *et al.* 1998, Ford and Ellis 1999). However, their role as a prey species for terrestrial predators such as wolves[2] (*Canis lupus*), coyotes (*Canis latrans*) (Steiger *et al.* 1989), and black bears[3] (*Ursus americanus*) is less well understood. Thus, the link between potential predation pressure and isolated haul-out site selection is not conclusive.

The distribution of black bears overlaps that of harbor seals along much of their coastal range in western Canada, but the bears are generally considered herbivorous, occasionally supplementing their diet with invertebrates (Pelton 1982) and salmon (Reimchen 2000). However, black bears are opportunistic predators and are quick to adapt to new feeding opportunities (*e.g.*, deer fawns (*Odocoileus* spp.), Matthews and Porter 1988; moose calves (*Alces alces*), Ballard *et al.* 1981; beavers (*Castor canadensis*), Smith *et al.* 1994). They may also occasionally take larger prey such as mature elk (*Cervus elaphus*) (Barmore and Stradley 1971) and adult moose (Austin *et al.* 1994), and black bears have been observed consuming seal carcasses along the coast in northern Labrador, although whether they killed them or were scavenging was unknown.[3]

Although studies of the in-air visual acuity of phocid seals are few, research on captive seals has shown that they are capable of identifying shapes and patterns (Renouf and Gaborko 1988, 1989) suggesting that only small amounts of visual detail are required for information processing. Furthermore, because captive seals can discriminate individual humans (Taylor *et al.* 1998), it is reasonable to expect that seals would have similar abilities when distinguishing potential threats in the wild.

I examined haul-out by Pacific harbor seals to (1) determine if there was a relationship between the abundance of seals at active haul-out sites and the distance to the source of potential terrestrial predators (mainland), distance to possible foraging depths, peripheral water depth, or haul-out areas, and (2)

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[3] Personal communication from I. Stirling, Canadian Wildlife Service, 5320 122 Street, Edmonton, Alberta T6H 3S5, Canada, November, 1999.

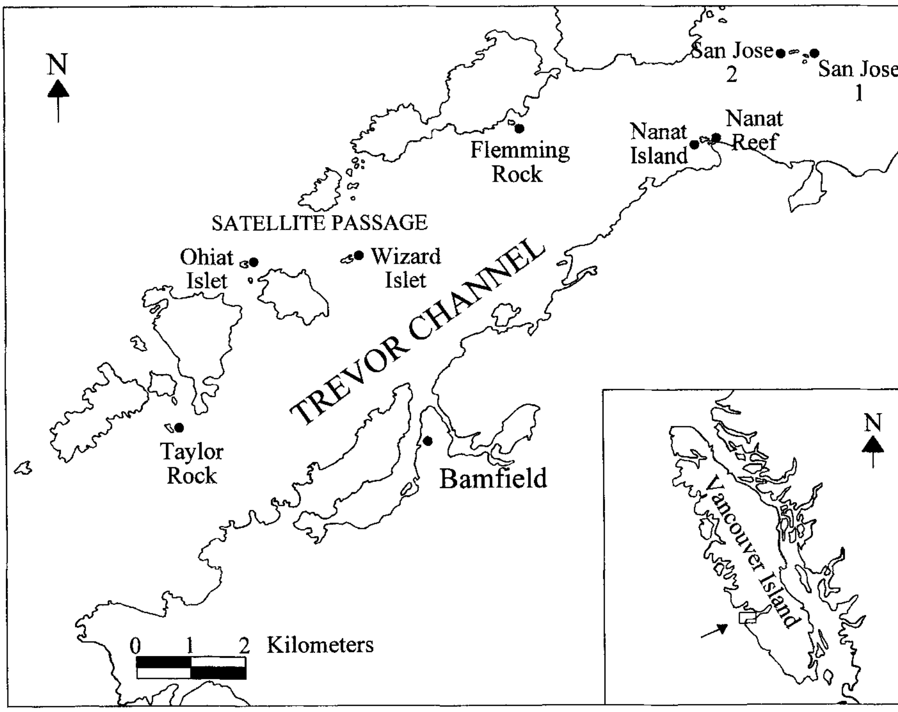

Figure 1. Map of Trevor Channel, British Columbia, showing locations of eight harbor seal haul-outs. Inset shows relative location along Vancouver Island coastline.

test whether harbor seals were capable of differentiating between a life-size black bear replica and a control object of similar size and color at a haul-out site.

Methods

Harbor Seal Abundance

The study area encompassed Trevor Channel in Barkley Sound near Bamfield, British Columbia where haul-out sites were located within the channel and the Deer Group archipelago bordering on mainland Vancouver Island (Fig. 1). Of the 14 sites monitored for harbor seals, eight locations were used as haul-outs in Trevor Channel. These included Nanat Reef, Nanat Island, San Jose Islets (two sites), Flemming Rock, Wizard Islet, Ohiat Islet, and Taylor Rock. A total of 14 surveys were conducted to determine seal abundance in Trevor Channel from a 4.3- or 4.9-m Cope aluminum boat using binoculars (Bushnell no. 13-730) from 17 October to 5 November 1999 and from 14 May to 3 June 2000. Censuses were completed within a two-hour time period to minimize the chance that individual seals would move among sites and be counted multiple times. Observations were standardized by conducting all counts within two hours of low tide and by using the same observer for each survey. Portions of individual surveys took place on both sides of low tide whenever possible, and survey routes were altered to avoid introducing timing-related biases to the census. Low tides were selected as the standard time as they coincided with the theoretical daily maximum of seals hauled out and available for counting (Schneider and Payne 1983, Pauli and Terhune 1987, Watts 1992).

Haul-out Characteristics

Isolation from terrestrial predators was defined as the distance to the mainland of Vancouver Island. The proximity of the haul-out site to shore was determined by measuring the nearest straight-line distance to the mainland from a hydrographic chart (Chart 3671, Canadian Hydrographic Service, Ottawa, ON, Canada) using a digital drafting table and MacMeasure™ computer software. Peripheral water depth at each haul-out was also obtained from this chart. Distances to foraging depths from the haul-outs were similarly calculated using the bathymetric contours in the channel from depths of 10 m to 100 m at 10-m intervals. Diet studies employing Time Depth Recorders (TDRs) (*e.g.,* Tollit *et al.* 1998, Lesage *et al.* 1999) have shown harbor seals use a range of foraging depths, therefore the proximity of water depths to the haul-out were examined separately to determine what depth, if any, could be related to the number of seals present. Haul-out area was examined as a potential confounding variable affecting seal abundance and was established from tape-measured haul-out lengths and heights (parallel and perpendicular to the water, respectively). The upper and lower boundaries of each haul-out were determined as the high tide line and the water's edge, respectively. Relationships among seal abundance and either distance to the coast, peripheral water depth, distance to foraging depths, or area of the haul-out were examined by linear regression techniques. Mean seal abundance at the study sites was transformed using the natural logarithm to conform to statistical assumptions, and results were considered significant at $P \leq 0.05$. The presence of black bears in the study area was confirmed by both visual observations of bears and their scats along the mainland coast.

Field Experiments

Field experiments were conducted at the harbor seal haul-out at Wizard Islet (49.51°N, 125.09°W). A total of 36 experimental trials took place from 7 to 22 November 1999 and from 7 May to 5 June 2000. Twelve replicates of three types of haul-out perturbations were conducted randomly: (1) researcher-only treatment, (2) rubber tire treatment, (3) bear model treatment. The researcher-only trials represented the baseline amount of disturbance common to all treatments created by the boat approach and the initiation of the experiment. The rubber tire trial involved leaving a black rubber tire (diameter = 80 cm) with a white Styrofoam core near the haul-out, which provided a model of approximate size to the frontal profile of an adult black bear, but

Table 1. Numbers of harbor seals at haul-out sites for 14 surveys in Trevor Channel during 17 October–5 November 1999 and 14 May–3 June 2000.

	Fall surveys									Spring surveys				
Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Nanat R.	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Nanat I.	0	2	0	0	0	2	0	0	0	0	0	1	1	0
Flemming R.	1	0	0	2	0	1	0	1	2	2	0	1	1	0
Taylor R.	2	1	0	2	1	3	1	0	1	0	0	2	0	0
San Jose 2	2	2	1	2	0	6	2	0	2	4	3	1	4	0
San Jose 1	4	12	8	7	5	0	1	8	9	10	6	7	6	3
Ohiat I.	3	14	26	22	16	12	13	23	19	20	19	16	18	8
Wizard I.	17	24	58	47	43	43	31	49	46	52	53	49	39	42
Total	29	55	93	82	65	68	48	81	79	88	81	78	69	53

was of unnatural form. The bear model trial involved leaving a full-sized bear replica 50 m from the haul-out to simulate the presence of a potential terrestrial predator.

In each trial the model or the controls were placed two hours prior to low tide (Time 1) and recovered immediately at low tide (Time 2). The rubber tire and the bear model were collected following each trial in which they were deployed to reduce the chance that the seals would habituate to the static objects. Individual seals were counted from the boat at a distance of approximately 50 m using binoculars at the beginning (Time 1) and the end (Time 2) of all treatments, which insured the changes in the number of seals corresponded to the two-hour treatment period only. The difference in the numbers of animals hauled out at Time 2 from Time 1 formed the basis of comparisons among treatment groups. A single factor ANOVA was used to test for differences in the number of seals hauled out for all treatments while a Tukey Test determined significant differences among treatment types (Zar 1984). Tide height was also examined at Time 2 (low tide) as a potential confounding variable as seal abundance may be positively correlated with low tide under natural conditions (Yochem *et al.* 1987).

Results

The total number of animals hauled out at individual study sites was variable across the surveys; however, the proportionate number of seals at the eight haul-outs remained relatively constant throughout the study period (Table 1). The mean number of seals was calculated for each haul-out site (n = 14, Table 2) and, because there were no significant differences between survey periods ($t = -0.71$, df = 12, $P = 0.49$), the data were pooled for analysis from both the fall and the spring seasons. The fewest numbers of harbor seals consistently occurred at Nanat Reef and Nanat Island, while the greatest abundance was found at Ohiat Islet and Wizard Islet.

There were no significant relationships between the distance to foraging

Table 2. Mean seal abundance, distance to shore, peripheral water depth, and haul-out area for 8 sites in Trevor Channel. Results of linear regressions of mean seal abundance (transformed by natural log) with haul-out characteristics are indicated.

Site	$\bar{x} \pm$ SE	Distance to shore (m)	Peripheral water depth (m)	Haul-out area (m^2)
Nanat R.	0.14 ± 0.09	13	4	54.6
Nanat I.	0.42 ± 0.20	103	5	86.8
Flemming R.	0.78 ± 0.21	2,506	10	502.2
Taylor R.	0.93 ± 0.27	1,920	20	136.5
San Jose 2	2.07 ± 0.46	1,999	10	887.5
San Jose 1	6.14 ± 0.90	1,938	10	411.5
Ohiat I.	16.4 ± 1.63	3,782	10	70.2
Wizard I.	42.4 ± 3.05	2,457	20	245.5
Statistic		$F_{1,6}$ = 8.56	$F_{1,6}$ = 2.71	$F_{1,6}$ = 0.53
P-value		0.03	0.15	0.49
r^2-value		0.59	0.31	0.08

habitat at depths of 10–100 m and the number of seals in Trevor Channel, as determined by multiple regression (range of Effect Tests $F_{1,6}$ = 0.25–3.36, P = 0.64–0.12) (Table 3). As such, no distances to possible foraging depths were included in further analyses. A multiple regression with the remaining explanatory variables did not pass the Whole Model test ($F_{3,4}$ = 2.24, P = 0.23). Subsequent examination of the variables determined that a lack of variation in the peripheral water depths and the effect of strong outliers in the haul-out areas of the study sites, combined with a small sample size, produced a poor fitting model as a whole, therefore, separate linear regressions were used. Seal abundance at haul-outs in Trevor Channel was found to be significantly related to the distance from shore ($F_{1,6}$ = 8.56, P = 0.03, r^2 = 0.59).

Table 3. Distance to 10 bathymetric contours, in meters, from 8 haul-out sites in Trevor Channel. The Effect Tests from a multiple regression of log mean seal abundance with distance to each depth are included.

Depth	Nanat Reef	Nanat Islet	Flemming Rock	Taylor Rock	San Jose 2	San Jose 1	Ohiat Islet	Wizard Islet	$F_{1,6}$	*P*
10 m	51	40	164	65	83	98	38	120	0.92	0.38
20 m	85	53	184	83	165	158	82	138	1.07	0.35
30 m	111	59	197	185	221	181	158	160	0.45	0.53
40 m	156	67	239	204	240	204	518	205	3.36	0.12
50 m	163	162	260	242	262	244	756	237	0.30	0.61
60 m	198	169	279	268	317	257	1025	263	0.61	0.47
70 m	237	175	303	357	376	276	1284	266	1.09	0.34
80 m	284	185	324	1564	388	282	1641	278	0.45	0.53
90 m	286	188	356	1846	400	299	1682	323	0.35	0.58
100 m	304	203	399	2677	412	321	1806	382	0.25	0.64

Table 4. Results from one-way ANOVA comparing differences in number of seals hauled out at Wizard Islet for all treatment types.

Source of variation	DF	SS	MS	F	P
Between treatments	2	3,696.2	1,848.1	52.6	<0.001
Residual	33	1,158.6	35.1		
Total	35	4,854.8			

The number of animals observed was not related to peripheral water depth ($F_{1,6}$ = 2.71, P = 0.15, r^2 = 0.31), and space was not a limiting factor at the haul-out sites as the mean number of seals observed was not influenced by the area of the haul-out ($F_{1,6}$ = 0.53, P = 0.49, r^2 = 0.08). The use of separate linear regressions was further justified by a *post hoc* forward stepwise regression (probability to enter = 0.250), which admitted distance to shore in the model ($F_{1,6}$ = 8.56, P = 0.03) but excluded peripheral water depth ($F_{1,6}$ = 0.52, P = 0.50) and area of the haul-out ($F_{1,6}$ = 0.06, P = 0.82).

Tide height was not significant when it was regressed against the number of seals hauled out at Time 2 during experimental trials ($F_{1,34}$ = 2.93, P = 0.103, r^2 = 0.158). However, the number of seals hauled out on Wizard Islet two hours following experimenter arrival was significantly affected by treatment at Time 1 (ANOVA $F_{2,33}$ = 52.6, P < 0.001, Table 4). The number of seals increased by 7–18 animals during the interval between Time 1 and Time 2 in the control treatments (n = 12) and by 5–16 animals during the tire treatments (n = 12). Conversely, the number of seals decreased by 2–18 animals in 11 of 12 of the experimental periods when the bear model was placed on the haul-out. In the eighth bear model trial, the number of seals increased from 53 to 56 animals. There were no significant differences between the number of seals hauled out following the intrusion of the researcher or the presence of the tire (Tukey Test = −0.02, P > 0.05) but there were significantly fewer seals hauled out after the model bear had been placed adjacent to the haul-out than after exposure to both the researcher (Tukey Test = 17.9, P < 0.05) and the tire (Tukey Test = 12.0, P = <0.05) (Fig. 2).

Discussion

Several hypotheses could be posited to explain the preference for harbor seals to haul out on offshore islands, including access to deeper water, proximity to foraging sites, and protection from terrestrial predators. In this study no significant relationship was found between the number of seals hauled out and the distance to possible foraging depths, peripheral water depth, or haul-out area, while an analysis of linear distances from shore correlated highly with the number of seals at eight haul-out sites. In addition, despite a relatively small sample size, the presence of a model black bear in a controlled experiment resulted in a significant reduction in the number of seals present compared to exposure to the researcher or to the presence of the control.

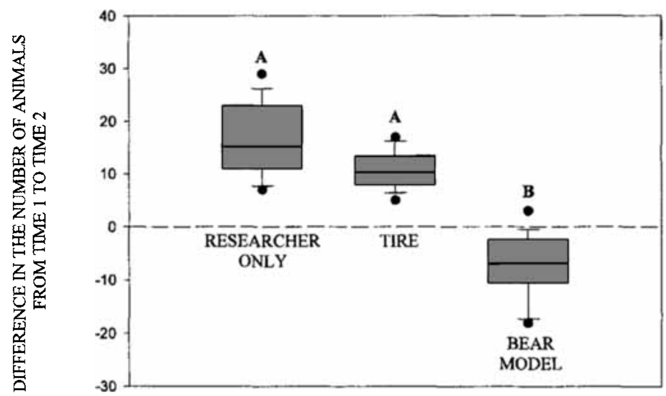

Figure 2. Difference in number of seals hauled out at Wizard Islet following three types of experimental trials (ANOVA; $F_{2,33} = 52.6$, $P < 0.001$, $n = 36$). Significant differences in pairwise comparisons between treatment types indicated by letters A and B (Tukey Test; $P < 0.05$).

The variable bathymetry and the relative proximity of the haul-outs to each other likely reduced any harbor seal foraging advantages gained by hauling out at one site over another in Trevor Channel. Fluctuating bottom depth characterizes most of the channel, making predictions of foraging habitat use extremely difficult. Bottom features and current likely have a greater effect on concentrating prey, and subsequently attracting seals, than does water depth at these depth ranges. Further telemetric studies of instrumented individuals would help determine the importance of haul-out site distance to particular water depths and to potential foraging grounds in Trevor Channel, as well as the rest of Barkley Sound.

Although the seal distribution data were significant ($P = 0.03$), they did not show a strong linear relationship to the distance from mainland Vancouver Island ($r^2 = 0.59$). Still, the choice of habitats was not a continuous one as the islands tended to be clumped near the coast or embedded within the Deer Group archipelago thereby negatively biasing an analysis of a linear nature. The effective distance for which predation risk from the coast structured harbor seal haul-out locations may also represent a confounding source of error. It is unlikely that seal abundance would continue to increase once a minimum degree of insularity from the mainland had been achieved, although the number of haul-outs in Trevor Channel are too few to examine this hypothesis more fully. Nevertheless, the results were suggestive that the distance to the coast is a consideration for haul-out site selection in harbor seals.

Experimentally increasing predation risk at Wizard Islet provided a direct test of the predator avoidance hypothesis. Captive harbor seals have demonstrated that visual cues can be used to execute pretrained behavioral sequences (Renouf and Gaborko 1988, 1989). This cognitive learning over time suggests that harbor seals comprehend simple rules upon which to base behavioral responses such as predator avoidance. However, requiring repeated conditioning to a potential predator is likely to be an unsuccessful survival strategy. Should prey species fail to distinguish predators upon encountering them, they may not survive the encounter to later associate the predator as a threat. Failure to avoid predators results in an abrupt end to any future contributions to fitness, and so there is strong selection pressure for individuals that are successful at avoiding and escaping from predators (Ydenberg and Dill 1986). It seems possible that harbor seals have an ontogenic behavioral response to predatory images much like naïve rabbits (Pongracz and Altbacker 2000), which would explain the drop in seal numbers in the presence of the predator model and the increase during the tire and the researcher-only treatments. Retaining this image directly through visual reinforcement would be possible given that black bears are seen foraging at beaches along Trevor Channel (personal observations). The single increase in the number of animals observed during the eighth bear model trial may be attributed to an anomaly wherein the seals hauled out on the southern face of the study site. The change in haul-out orientation resulted in the predator model, which had been placed on the northern expanse of the haul-out, being out of the line of sight of the animals. A return to the traditional haul-out location resulted in continued decreases in the number of seals during the remaining four bear trials, suggesting the move was an irregularity and did not represent a habituation to the static model. Harbor seals at Wizard Islet are subject to a high degree of disturbance from commercial trawlers and recreational boats, particularly during the summer months when boat traffic through Satellite Passage (Fig. 1) increases. This may have predisposed these seals to haul out after a disturbance of any kind but does not account for the differences in seal abundance after the three treatments.

Few studies have attempted to quantify the role of terrestrial predation in the pinniped life cycle. Stirling (1977) contrasted the behavior of Arctic ringed seals (*Phoca hispida*) with the Antarctic Weddell seals (*Leptonychotes weddelli*) as the two species occupy ecologically similar habitat in the presence or absence of terrestrial predators. There were significant differences between the two species in their distribution and mating patterns which could be attributed to pressures from polar bears (*Ursus maritimus*), Arctic foxes (*Alopex lagapus*), and wolves or the lack of terrestrial predators in the case of ringed and Weddell seals, respectively. The selection of isolated haul-out sites by the more temperate Pacific harbor seals increases their insularity from terrestrial carnivores and can be interpreted as another phocid behavioral adaptation to avoid contact with predators.

Harbor seals in Trevor Channel hauled out in increasing numbers as distance from the coast increased, and seals at Wizard Islet were seemingly indifferent to researcher and control treatments but abandoned the haul-out in the presence of the bear model. This may apply to other nearshore marine environments where a continuum of suitable haul-outs are available and should be further researched. Harbor seals may indeed alter their use of haul-outs, particularly during the breeding season or to better access prey as has been reported, however, selection of these isolated sites and their continued use may represent a behavioral adaptation to avoid terrestrial predators.

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Literature Cited

Austin, M. A., M. E. Obbard and G. B. Kolenosky. 1994. Evidence for a black bear, *Ursus americanus,* killing an adult moose, *Alces alces.* The Canadian Field-Naturalist 108:236–238.

Ballard, W. B., T. H. Spraker and K. P. Taylor. 1981. Causes of neonatal moose calf mortality in south central Alaska. Journal of Wildlife Management 45:335–342.

Barmore, W. J., and D. Stradley. 1971. Predation by black bear on mature elk. Journal of Mammalogy 51:199–202.

Brown, R. F., and B. R. Mate. 1983. Abundance, movements and feeding habits of harbor seals, *Phoca vitulina,* at Netarts and Tillamook Bays, Oregon. Fishery Bulletin, U.S. 81:291–301.

Da Silva, J., and J. M. Terhune. 1988. Harbour seal grouping as an anti-predator strategy. Animal Behaviour 36:1309–1316.

Ford, J. K. B., and G. M. Ellis. 1999. Transients: Mammal hunting killer whales of British Columbia, Washington, and Southeastern Alaska. University of British Columbia Press, Vancouver, BC.

Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm and K. C. Balcomb. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology 76:1456–1471.

Härkönen, T. J. 1987. Influence of feeding on haul-out patterns and sizes of subpopulations in harbour seals. Netherlands Journal of Sea Research 21:331–339.

Lesage, V., M. O. Hammill and K. M. Kovacs. 1999. Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. Canadian Journal of Zoology 77:74–87.

Lima, S. L., and L. M. Dill. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Matthews, N., and W. Porter. 1988. Black bear predation on white-tailed deer neonates in the central Adirondacks. Canadian Journal of Zoology 66:1241–1242.

Pauli, B. D., and J. Terhune. 1987. Meteorological influences on harbour seal haulout. Aquatic Mammals 13:114–118.

Pelton, M. R. 1982. Black bear. Pages 505–514 *in* J. Chapman and G. Feldhamer, eds. Wild Mammals of North America. The John Hopkins University Press, Baltimore, MD.

Pitcher, K. W., and D. C. McAllister. 1981. Movement and haul-out behaviour of radio-tagged harbour seals, *Phoca vitulina.* Canadian Field-Naturalist 95:292–297.

Pongracz, P., and V. Altbacker. 2000. Ontogeny of the responses of European rabbits

(*Oryctolagus cuniculus*) to aerial and ground predators. Canadian Journal of Zoology 78:655–665.

REIMCHEN, T. E. 2000. Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. Canadian Journal of Zoology 78:448–457.

RENOUF, D., AND L. GABORKO. 1988. Spatial matching to sample in harbour seals (*Phoca vitulina*). Biology of Behaviour 13:73–81.

RENOUF, D., AND L. GABORKO. 1989. Spatial and visual rule use by harbour seals (*Phoca vitulina*). Biology of Behaviour 14:169–181.

RENOUF, D., AND J. W. LAWSON. 1986. Harbour seal vigilance: Watching for predators or mates? Biology of Behaviour 11:44–49.

RIEDMAN, M. 1990. The pinnipeds: Seals, sea lions, and walruses. University of California Press, Berkeley, CA.

SCHNEIDER, D. C., AND P. M. PAYNE. 1983. Factors affecting haul-out of harbor seals at a site in southern Massachusetts. Journal of Mammalogy 64:518–521.

SMITH, D. W., D. R. TRAUBA, R. K. ANDERSON AND R. O. PETERSON. 1994. Black bear predation on beavers on an island in Lake Superior. American Midland Naturalist 132:248–255.

STACEY, P. J., AND R. W. BAIRD. 1989. Harbour seal reactions to killer whales. The Victoria Naturalist 45:16–17.

STEIGER, G. H., J. CALAMBOKIDIS, J. C. CUBBAGE, D. E. SKILLING, A. W. SMITH AND D. C. GRIBBLE. 1989. Mortality of harbor seal pups at different sites in the inland waters of Washington. Journal of Wildlife Diseases 25:319–328.

STIRLING, I. 1977. Adaptations of Weddell and ringed seals to exploit the polar fast ice habitat in the absence of presence of surface predators. Pages 741–748 *in* G. A. Llana, ed. Proceedings of the third symposium on Antarctic biology, Washington, DC. 1,252 pp.

STIRLING, I. 1983. The evolution of mating systems in pinnipeds. Pages 489–527 *in* J. F. Eisenburg and D. G. Kleiman, eds. Recent advances in the study of mammalian behaviour. American Society of Mammalogy Special Publication Number 7.

SURYAN, R. M., AND J. T. HARVEY. 1998. Tracking harbor seals (*Phoca vitulina richardsi*) to determine dive behaviour, foraging activity, and haul-out site use. Marine Mammal Science 14:361–372.

TAYLOR, A. A., H. DAVIS AND G. J. BOYLE. 1998. Increased vigilance towards unfamiliar humans by harbor (*Phoca vitulina*) and gray (*Halichoerus grypus*) seals. Marine Mammal Science 14:575–583.

THOMPSON, P. M., D. MILLER, R. COOPER AND P. S. HAMMOND. 1994. Changes in the distribution and activity of female harbour seals during the breeding season: Implications for their lactation strategies and mating patterns. Journal of Animal Ecology 63:24–30.

TOLLIT, D. J., A. D. BLACK, P. M. THOMPSON, A. MACKAY, H. M. CORPE, B. WILSON, S. M. VAN PARIJS, K. GRELLIER AND S. PARLANE. 1998. Variations in harbour seal *Phoca vitulina* diet and dive depths in relation to foraging habitat. Journal of Zoology (London) 244:209–222.

VAN PARIJS, S. M., P. M. THOMPSON, D. J. TOLLIT AND A. MACKAY. 1997. Distribution and activity of male harbour seals during the mating season. Animal Behaviour 54:35–43.

WALKER, B. G., AND W. D. BOWEN. 1993. Behavioural differences among adult male harbour seals during the breeding season may provide evidence for reproductive strategies. Canadian Journal of Zoology 71:1585–1591.

WATTS, P. 1992. Thermal constraints on hauling out by harbour seals (*Phoca vitulina*). Canadian Journal of Zoology 70:553–560.

YDENBERG, R. C., AND L. M. DILL. 1986. The economics of escaping from predators. Advances in the Study of Behaviour 16:229–249.

YOCHEM, S., B. S. STEWART, R. L. DELONG AND D. P. DEMASTER. 1987. Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in autumn. Marine Mammal Science 3:323–332.

ZAR, J. H. 1984. Biostatistical analysis. Second Edition. Prentice-Hall, Englewood Cliffs, NJ.

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