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Harbour seal vigilance decreases over time since haul out

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Abstract. The hypothesis was examined that vigilance of harbour seals, *Phoca vitulina*, on haul-out sites decreases with time since haul out. The study was conducted in the Bay of Fundy, Canada, where the seals haul out onto newly exposed rocky ledges on falling tides. Initial scanning time of newly hauled-out harbour seals during the first 3 min after haul out decreased as group size increased. The scanning times of individual seals significantly decreased over time since haul out. Alternating observations (similar conditions for each pair of seals) showed that newly hauled-out seals scanned significantly longer than seals that were resident for over 30 min. Seals on the periphery of the group scanned significantly longer than those in the centre. Part of the scanning decrease of seals in larger groups was attributed to time since haul out and fewer animals being on the periphery of the group. The seals were 1.4 ± 0.6 (SD) body lengths from the water's edge and 1.6 ± 0.5 body lengths apart; 81% were oriented towards the water; this orientation and spacing allowed for ready access to the water. These behaviour patterns, and the high levels of vigilance, support an anti-predator function of harbour seal grouping on haul-out sites. © 1996 The Association for the Study of Animal Behaviour

Harbour seals, *Phoca vitulina*, regularly haul out onto offshore ledges, bars or isolated beaches (Terhune & Almon 1983; Krieber & Barrette 1984; Godsell 1988). They usually come completely out of the water and lie quietly for a few hours. In areas of high tidal amplitude (6–8 m), such as the Bay of Fundy, Canada, most haul-out sites are exposed on a falling tide (Terhune & Almon 1983; Pauli & Terhune 1987). In areas with less tidal amplitude, seals may haul out on exposed ledges or beaches throughout the day (Renouf & Lawson 1986; Godsell 1988).

Possible advantages of hauling out include rest (Krieber & Barrette 1984), thermoregulation to augment the moulting process (Ling et al. 1974) and predator avoidance (da Silva & Terhune 1988). On haul-out sites in the Bay of Fundy, harbour seals spend much of their time resting (58.3%) or scanning (41.3%). Moving and interacting with other seals is infrequent (0.4%; da Silva & Terhune 1988).

The formation of groups has often been regarded as a predator avoidance mechanism (Powell 1974; Siegfried & Underhill 1975; Bertram 1978). Harbour seals in the Bay of Fundy are subject to regular human disturbances, including shooting (Terhune 1985a). Humans have hunted seals for many hundreds of years, and human disturbance usually results in the seals raising their heads and sometimes rushing into the water (Venables & Venables 1955). Bears, *Ursus americanus*, and other large carnivores (possibly wolves, *Canis* sp. and eastern panthers, *Felis concolor*) were likely natural predators of harbour seals on haul-out sites.

The time that individual harbour seals spend visually scanning their surroundings decreases with increasing group size (Krieber & Barrette 1984; Terhune 1985a). At Miquelon (French islands south of Newfoundland), harbour seal vigilance decreases within an hour after the group reaches its maximum size (Renouf & Lawson 1986). In the Bay of Fundy, on a falling tide, the sizes of harbour seal groups on haul-out sites usually increase slowly over time (Terhune & Almon 1983; Pauli & Terhune 1987; da Silva & Terhune 1988). If harbour seals have a high rate of scanning immediately following haul out and then reduce their individual vigilance, the apparent effect would be a reduction in the average

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scanning time as group size increases. In this study we examined the hypothesis that vigilance of harbour seals decreases with the time since haul out.

Animals at the edge of a group have a greater risk of predation than those in the centre (Hamilton 1971). Among mammals, peripheral individuals are more vigilant than central ones (Hoogland 1979; Quenette 1990; Burger & Gochfeld 1992). We briefly compared the scanning times of seals at the periphery and centre of the groups. Using aerial photographs, we also examined the orientation and spacing of seals on haul-out sites.

METHODS

Harbour seals were observed on the Shag Rocks, Saint John, New Brunswick (45°14′N, 66°04′W: see Terhune & Almon 1983). The rocky ledges where the seals haul out are 0.5–1 km from a clifftop observation site. The seals were observed using a 20–45 × telescope and 7 × 50 binoculars. We could not recognize individuals. Observations were made between 1000 and 2000 hours, on a falling tide when it was not raining or foggy. The study was conducted from 20 June to 18 October 1992.

We defined a scan as any movement that increased the visual field of the seal. Typically the seal raised its head from a resting position, held it high while moving it horizontally and then lowered it to the original resting position. We could not measure vigilance when seals scanned without raising their heads.

A single observation period consisted of measuring (using cumulative-time stopwatches) the total scan time of a seal during 3 min. This observation period was followed by a 3-min interval when the seal was not observed. During this interval we counted the size of the group. An observation session consisted of the periods and intervals of observation on a single day.

At the beginning of each observation session, we selected a focal animal that had just hauled out. The scanning times of this seal were observed for five consecutive observation periods and intervals (30 min total elapsed time). After an arbitrary time of 30 min, we chose another focal animal that had just hauled out (if available). If no seal had recently hauled out, we continued observations on the original focal animal until we could select a second subject.

Once we located a second seal, we then alternated the observations between the second subject and the initial focal animal. Thus we could compare the scanning time of a newly hauled-out seal under similar conditions to the scanning time of a seal that had been hauled out for at least 30 min. This procedure continued as long as both seals remained on the haul-out site. If one subject left the haul-out site, the remaining seal became the focal animal. We observed it (3-min observation periods with 3-min intervals) for 30 min (or more) since its haul-out time, and then selected another newly hauled-out seal. Again, we alternated observations between the newly hauled-out seal and the seal that had been hauled out for at least 30 min.

Paired *t*-tests were performed on (1) the first and last scan durations of all seals, (2) the first and fifth (arbitrarily chosen) scans (and group sizes) of individual seals, (3) the scan durations (and group sizes) of seals that had been hauled out for at least 30 min and the initial scan (and group sizes) of new arrivals, and (4) all alternating measures of scan durations (and group sizes) of seals that had been hauled out for at least 30 min and the adjacent measures from the recently hauled-out seal. We performed a linear regression to examine the relationship between initial scan durations and length of stay of the seals on the haul-out site.

On 3 consecutive days (12–14 July 1993) we compared the scanning times of seals at the periphery of the groups with those in the centre. Observation sessions began 3.5 h before low tide and continued until low tide. We observed seals that appeared to be dry (i.e. had probably been hauled out for 15–20 min or more). We selected pairs of seals, one near the periphery of the group and one near the centre, and observed them for 3 min each, as before. By noting each animal's location within the group, we took care not to pick the same seals during subsequent measurements.

In association with aerial censuses (Terhune 1985b; Colbourne & Terhune 1991), we took photographs of groups of 10 or more harbour seals on haul-out sites from a low-flying aircraft. These surveys were conducted between 23 February and 20 December of 1984 and 1987. The haul-out sites were along the New Brunswick coast of the Bay of Fundy.

From photographs, we examined the orientations of the seals with respect to the water's

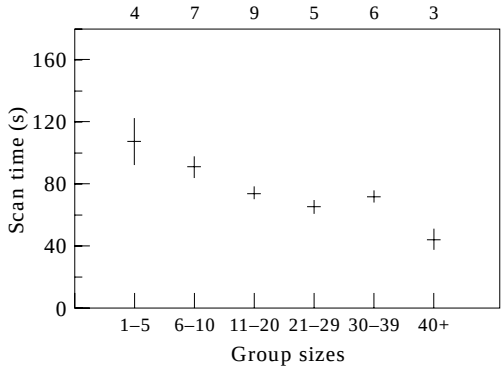

Figure 1. Mean ± SE scan times of harbour seals per 180-s time period relative to arbitrary group sizes on the haul-out site. The sample sizes are given above each point.

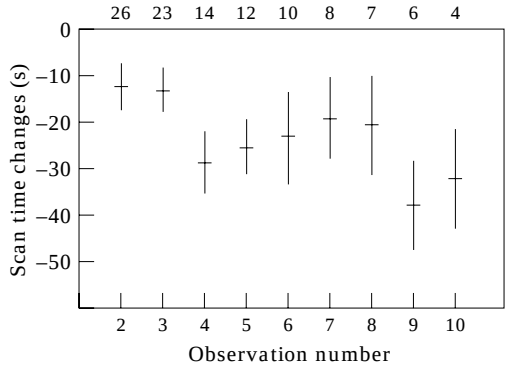

Figure 2. Mean ± SE scan time changes of harbour seals over elapsed time since haul out, relative to the initial scan duration per 180 s of each animal. Each 3-min observation period was separated by a 3-min interval. The sample sizes are given above each point.

edge. We allocated the direction of the seal's body to one of six equal 60° segments. The segments were numbered clockwise, with segment 1 centred perpendicular to the shoreline. Thus segments 1, 2 and 6 faced in the direction of the water; segments 3–5 faced landward. Chi-squared tests examined the orientation of the seals on each photograph and overall.

We also noted the distances of the seals from the water's edge and the distances of the nearest neighbours. All distances are expressed in terms of adult seal lengths. Photographs were taken at different heights and angles, so absolute distance measurements were not possible.

RESULTS

We observed scanning seals on 9 days between 29 June and 4 October 1992. On 8 other observation days (e.g. 20 June), seals did not haul out. Only 34 seals were observed to haul out at appropriate times during the study. Not all seals remained on the haul-out site throughout the observation session. Some seals were observed to swim back and forth in front of the haul-out site before hauling out.

The average scanning times per arbitrary group size increments decreased as group size increased (Fig. 1). The durations of initial scans ranged between 42 and 150 s per 180-s observation period ($\bar{X} \pm \text{SD} = 93.3 \pm 24.4$, $N = 34$). The initial scan time varied negatively with the group size ($r = -0.53$, $F_{1,32} = 12.189$, $P = 0.001$).

The initial scan duration was significantly longer than the last scan duration measured per seal ($t = 172.63$, $df = 33$, $P < 0.001$). Consecutive observations of single seals indicated a decrease in scanning over time. Only two of the 34 seals observed had initial scan durations shorter than their final scan duration. For those seals still hauled out after 27 min, the first scans were significantly longer than their fifth scans ($t = 4.58$, $df = 9$, $P = 0.001$) even though the group sizes had not significantly changed ($t = -0.80$, $df = 9$, $P = 0.45$).

There were significant differences between the fifth scan of a resident seal and the first scan of a new arrival ($t = -5.26$, $df = 9$, $P = 0.005$) without accompanying changes in the group sizes ($t = 0.98$, $df = 9$, $P = 0.39$). Significant differences also occurred when alternating measurements were obtained between a seal that had been hauled out for over 30 min and a new arrival that remained on the haul-out site for more than a single observation time. The scan times of the longer hauled-out seals were shorter than those of the new arrivals ($t = 2.33$, $df = 29$, $P = 0.03$) and the group sizes (between adjacent pairs of measurements) did not differ ($t = 0.25$, $df = 29$, $P = 0.81$). Initial scan times were not related to the length of stay on the haul-out site ($r^2 = 0.02$, $df = 32$).

The scanning time changes of all seals were normalized to reflect increases or decreases relative to that animal's initial scan immediately following haul out (Fig. 2). There was a decrease in scanning of over 10 s (per 180-s observation

time) over the first 6 min. Longer sets of observations indicated that the scanning time generally decreased with time since haul out but did not drop to zero (Fig. 2).

Weather conditions favoured optimal haul-out conditions during the peripheral versus centre scanning study. On all three days there was sunshine, warm temperatures and very little wind. There were also no human disturbances, and the seals did not flush from the haul-out sites during these observation sessions.

The seals formed up to four simultaneous groups during these observation sessions. One or two haul-out sites were abandoned and the seals moved to other, lower sites as the tide fell. Thus, seals were arriving (from other sites or from the open water) at haul-out sites throughout the study session. Newly arrived seals tended to haul out where there was available space. Typically this was at either end of the group (they tended to form narrow groups parallel to the water line) or near the front centre if the falling tide exposed a sufficiently large area that permitted the newcomer to haul out without having to displace a resident seal.

The scanning rates of the seals on these 3 days were lower than average. Three of the observed seals did not scan at all during the 3-min observation period. Seals on the periphery scanned an average ± SD of 38.5 ± 17.4 s per 3 min period, but those in the centre scanned only 17.2 ± 9.1 s. A paired *t*-test indicated a significant difference between the scan times of these two groups ($t = 5.99$, $df = 41$, $P < 0.0001$).

We examined 87 photographs from aerial surveys. There were 40.4 ± 23.1 seals per haul-out site (range 10–107). The seals were 1.4 ± 0.6 (range 0–12) body lengths from the water's edge and 1.6 ± 0.5 (range 1–22) body lengths apart. The seals oriented towards the water while on the haul-out sites. The numbers of seals per sector were 1361, 628, 212, 165, 231 and 578 for sectors 1–6, respectively. Chi-squared tests indicated a random seal orientation in 12 photographs ($P > 0.05$), and non-random orientation in 75 of the photographs ($P < 0.05$). The overall distribution was non-random ($\chi^2 = 820.39$, $df = 5$, $P < 0.0001$).

DISCUSSION

We could not identify individual seals, so the same animal may have been observed more than once. On any one day the number of seals observed was low; to avoid observing them twice, we noted their location on the haul-out site. A focal seal could have re-entered the water and hauled out again at the appropriate time to become a second subject, however.

The probability of observing the same seal on different days was low. Only four of the 34 observations were made with group sizes below five seals. Thus even if a particular seal was likely to haul out before the others, we would not have repeatedly selected it as a focal animal. Harbour seals also form unstable groups on haul-out sites and disband after the haul-out period (da Silva & Terhune 1988). In the Bay of Fundy, harbour seals regularly move between haul-out sites (Terhune & Almon 1983; Colbourne & Terhune 1991). It is likely that many different seals were hauling out at our observation site throughout the study; thus, the probability of observing the same seal twice was low.

Scanning Rate and Group Size

As group size increased, the scanning times of individual harbour seals decreased (Fig. 1). This result supports previous observations obtained outside the breeding season (Krieber & Barrette 1984; Terhune 1985a; da Silva & Terhune 1988; cf. Renouf & Lawson 1986). During the breeding season, adult male harbour seals at Miquelon increased their scanning behaviour with increasing group size, possibly in association with mating behaviour patterns (Renouf & Lawson 1986). Most of the data for this study were obtained following the mating season and thus do not fully address the hypothesis presented by Renouf & Lawson (1986).

An implication of the finding that initial scans varied negatively with group size is that the seals may be able to assess approximate group sizes by first scanning the haul-out site before hauling out.

There was no relationship between the duration of the initial scan and the length of time the seal remained hauled out. Thus the observations that scanning times decreased over time since haul out were not compromised by particularly vigilant seals vacating the haul-out site sooner than less vigilant ones.

Harbour seal vigilance was highest immediately after haul out and dropped to a lower level (but usually not to zero) within half an hour (Fig. 2).

Variability in the data in Fig. 2 may be due to the influence of different group sizes, smaller sample sizes and meteorological variables (e.g. wind, waves).

The pattern of decrease in vigilance over time was evident when single animals were examined over time or a pair of seals was examined sequentially. The measures that alternated between seals that had been hauled out for half an hour or more and new arrivals examined these pairs of seals under similar conditions, with no significant changes in group sizes. These data suggest that temporal factors are important but do not consider the possible influence of location within the group.

Scanning Rate and Relative Position

Seals in the water located an unoccupied area on which to haul out, which was typically near the water's edge and thus at the periphery of the group. The increased scanning rate at the periphery of the group was probably a result of the disturbance associated with the arrival of new seals and presumably potential competition for space. Because harbour seals tended to haul out at the extremities of the group or onto areas within the group that had been exposed recently by the falling tide, they appeared to select space not already occupied by another seal. Seals in the centre of the group were typically further back from the water's edge and had been hauled out for some time. By selecting seals with dry coats for observation, we reduced the bias associated with time since haul out on scanning time.

Animals on the edge of a group are more likely to be preyed upon than those in the centre (Hamilton 1971). An edge effect has been described for cliff swallows, *Hirundo pyrrhonota* (Brown & Brown 1987), prairie dogs, *Cynomys* spp. (Hoogland 1979), coati, *Nasua narica* (Burger & Gochfeld 1992) and other species (Elgar 1989; Quenette 1990). For harbour seals, however, the greater vigilance at the edge of the group appears to be also related to the activity associated with arriving newcomers. As group size increases, particularly when the seals are hauling out along a straight ledge, more seals are positioned in the centre and front middle, which lowers average scanning by the group members because of the smaller proportion of seals on the periphery. In a smaller group (five or fewer), most seals would be considered peripheral, which may explain part of the increased vigilance of seals in small groups.

Anti-predator Functions of Haul Out

Observations by Renouf & Lawson (1986) question the anti-predator function of harbour seal haul out during the breeding season. Harbour seal scanning may be associated with watching for mates or another function not related to predation (Renouf & Lawson 1986; Quenette 1990). An anti-predator function of seal grouping (da Silva & Terhune 1988) requires that the seals remain close to the water's edge to facilitate escape. By observing the locations of seals on haul-out sites, we examined a hypothesis that the orientation of seals on haul-out sites favoured individual escape to the sea.

At the Shag Rocks, a consequence of a tidal amplitude of 7 m is that the exposed area increased from 0.1 ha at high tide to approximately 5.8 ha near low tide (Terhune & Almon 1983). As with all other haul-out sites within the Bay of Fundy, once a seal hauls out, it must move continually down the rocks to remain near the water's edge. The nearness of the seals to the water's edge and their spacing, especially given the uneven topography of many haul-out sites, suggests that they continually relocated their position on the haul-out site.

Harbour seals have gregarious tendencies on land but do not tolerate being touched (Sullivan 1982). Except for pregnant or lactating females who were more widely spaced, adults and juveniles maintained inter-animal distances of 0.9 m (0.5 body lengths) on the sand beaches of Miquelon (Davis & Renouf 1987). The greater inter-animal distances noted in this study are probably related to the uneven topography of the rocky haul-out sites, which often precluded closer spacing without touching.

The location and orientation of seals on haul-out sites favours escape into the water. The seals were close enough to the water and far enough apart to usually avoid colliding with each other when they flushed. When a group was disturbed, it was not uncommon for the seals to suddenly rush to, or into, the water. Inter-animal spacing was reduced at these times, but not to the point that the seals were all touching or colliding with each other.

If members of a group coordinate their vigilance and use vocalizations to alert conspecifics of

danger, then the time spent scanning for predators can be reduced for all but a few sentinels. This is the 'watchman's song' hypothesis (Wickler 1985). Sentinel systems have been described for meerkats, *Suricata suricatta* (Moran 1984), and Florida scrub jays, *Aphelocoma coerulescens* (McGowan & Woolfenden 1989), but not dark-eyed juncos, *Junco hyemalis* (Lima 1995). We have no evidence that harbour seals coordinate their vigilance activities. The high individual levels of vigilance (Terhune 1985a; Fig. 1) indicate that all members of the group remained alert while on the haul-out site. Unlike meerkats and Florida scrub jays, harbour seal groups are larger and do not have permanent members (Terhune & Almon 1983; da Silva & Terhune 1988). Coordination of vigilance behaviour would be difficult to achieve in non-social groups.

When a single seal was disturbed and rushed towards the water, all of the other members of the group did likewise. If peripheral seals were vigilant only to locate mates (Renouf & Lawson 1986) or to detect approaching conspecifics who might displace them from their location on the haul-out site, we would not expect the entire group to react to the actions of a single seal. The result supports the anti-predator function of harbour seal vigilance.

Vigilance of individual harbour seals on haul-out sites decreases with increasing group size (Krieber & Barrette 1984; Terhune 1985a; this study) and time since haul out, although group vigilance increases with increasing group size (da Silva & Terhune 1988). Seals near the periphery of the group are more vigilant than those within the centre. The spacing behaviour of the seals results in improved detection of escape behaviour by neighbours while avoiding crowding during escape into the water. Thus vigilance and orientation of harbour seals in the Bay of Fundy supports an anti-predator function of grouping on haul-out sites. This function does not preclude simultaneously scanning for mates during the breeding season, as suggested by Renouf & Lawson (1986).

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