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PROBABILITY OF DETECTING HARBOR PORPOISE FROM AERIAL SURVEYS: ESTIMATING $g(0)$

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Abstract: Harbor porpoise (*Phocoena phocoena*), and most other cetaceans, spend a significant proportion of time submerged, and are undetectable from the air. Abundance estimates based on line transect sampling may be severely biased by assuming that all porpoise near the line are detected [$g(0) = 1$]. By tracking groups of harbor porpoise from land, we estimated the proportion of time harbor porpoise spent at the surface and the probability that aerial observers detected groups within 200 m of the transect line. Two teams on land, equipped with electronic theodolites, tracked harbor porpoise while surveys were conducted from an aircraft equipped with side-bubble windows and a belly window. During 7 days, 33 hours of observation were made in a high-density area for harbor porpoise near Orcas Island, Washington. We monitored 7 different harbor porpoise groups from 15 to 66 minutes each. The average proportion of time at or near the surface was 0.231 (SE = 0.032). From a selected sample of 164 land-based sightings of harbor porpoise groups, 50 (30.5%) were observed from the aircraft. For our aerial line transect surveys of harbor porpoise conducted by experienced observers, $\hat{g}(0) = 0.292$ (SE = 0.107). However, for the inexperienced observers, $\hat{g}(0)$ was 0.079 (SE = 0.046), which demonstrates the importance of experience and training.

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Key words: aerial surveys, dive behavior, $g(0)$ estimation, harbor porpoise, line transect sampling, *Phocoena phocoena*, visibility bias.

Visibility bias in aerial surveys typically leads to underestimation of animal abundance. Marsh and Sinclair (1989) classify the causes of visibility bias for marine mammals into 2 categories: availability bias represents undercounting of animals that are missed because they are submerged, and perception bias represents undercounting of visible animals that are missed for a variety of other reasons (e.g., distance, cloud cover, sun glare, observer fatigue). Pollock and Kendall (1987) review different methods of estimating visibility bias. One such method, line transect sampling (Buckland et al. 1993), is based on an assumption that all animals on a line are seen [$g(0) = 1$], and visibility bias away from

the line is estimated from observed distances. Clearly, $g(0)$ is not unity for surveys of marine mammal species that spend longer periods of time underwater than the time the observer views the surface (Hiby and Hammond 1989, Buckland et al. 1993). Recent efforts have been made to estimate $g(0)$ with breath rate data (Leatherwood et al. 1982, Barlow et al. 1988, Raum-Suryan 1995), multiple independent observers (Barlow 1988, Polacheck and Smith 1989, Oien 1990, Rugh et al. 1993, Palka 1995), multiple ships (Schweder et al. 1991b), and concurrent aerial and ship surveys (Buckland and Turnock 1992).

Calambokidis et al. (1992), Green et al. (1992),

and Barlow et al. (1988) recognized that availability bias is critical for aerial surveys of harbor porpoise. Barlow et al. (1988), using data from several studies of harbor porpoise breath rate, estimated that harbor porpoise were at the surface 23.9% of the time and, given certain assumptions, estimated that $g(0) = 0.31$ if all porpoise at the surface were detected (i.e., no perception bias). Kraus et al. (1983) conducted concurrent ship, ground, and aerial surveys in a narrow channel with high densities of harbor porpoise and estimated that aerial observers saw 14% of the harbor porpoise. By the nature of the experiment, their estimate included both availability and perception bias; however, observations were from a 630-m strip, and the effect of distance from the line was not considered. We conducted a similar experiment to estimate $g(0)$ for aerial surveys of harbor porpoise by incorporating both availability bias and perception bias, while specifically examining factors that affect perception bias.

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METHODS

We conducted the sighting experiment off Point Doughty on the northwest side of Orcas

Island in the San Juan Islands, Washington (Fig. 1). This site was selected based on the high density of harbor porpoise, viewing conditions, and the viewing distance and angle for the land-based observers, which was more than 180° extending from the north side of Orcas Island to the southwest down President Channel. The site was located about 17 m above the mean lower low water (MLLW) tidal level.

Aerial Survey Procedures

We conducted aerial surveys for 33 hours on 7 days during 3–13 August 1992. The first 2 days were used as a training period and were not included in the analysis. The survey platform was a twin-engine, high-wing aircraft (Partenavia P-68) outfitted with bubble windows for side observation and a belly window to search below the aircraft. Surveys were flown at 183 m (600 ft) altitude and at an air speed of 185 km/hour (100 knots). A total of 547 transects were flown in alternating easterly and westerly directions, 3.5–5.5 km long, all situated 0.2–3.3 km north of the land observation site (Fig. 1).

Three observers (left, right, and center) searched for animals while a fourth person, in the copilot seat, recorded data and navigated. Six different observers were used throughout the experiment: 4 were experienced at searching for harbor porpoise from the air, one observer had prior aerial survey experience but not with harbor porpoise, and one observer had no experience with aerial surveys. The latter 2 observers were classified as inexperienced at searching for harbor porpoise. Experienced observers were stationed at side windows or the belly window, while the 2 inexperienced observers were only stationed at the belly window. The land-based observers maintained communication with the data recording person who navigated the plane along specific latitudes. Observers were unaware of the communication, and changes in transect lines did not necessarily alert the observers because harbor porpoise were not seen on most lines.

We recorded data with a laptop computer that received position data directly from the LORAN navigation system. We recorded aircraft position at the beginning and end of transect lines, for a course change, and when porpoise were sighted. We recorded weather and sea conditions whenever conditions changed. Surveys were limited to good weather and were

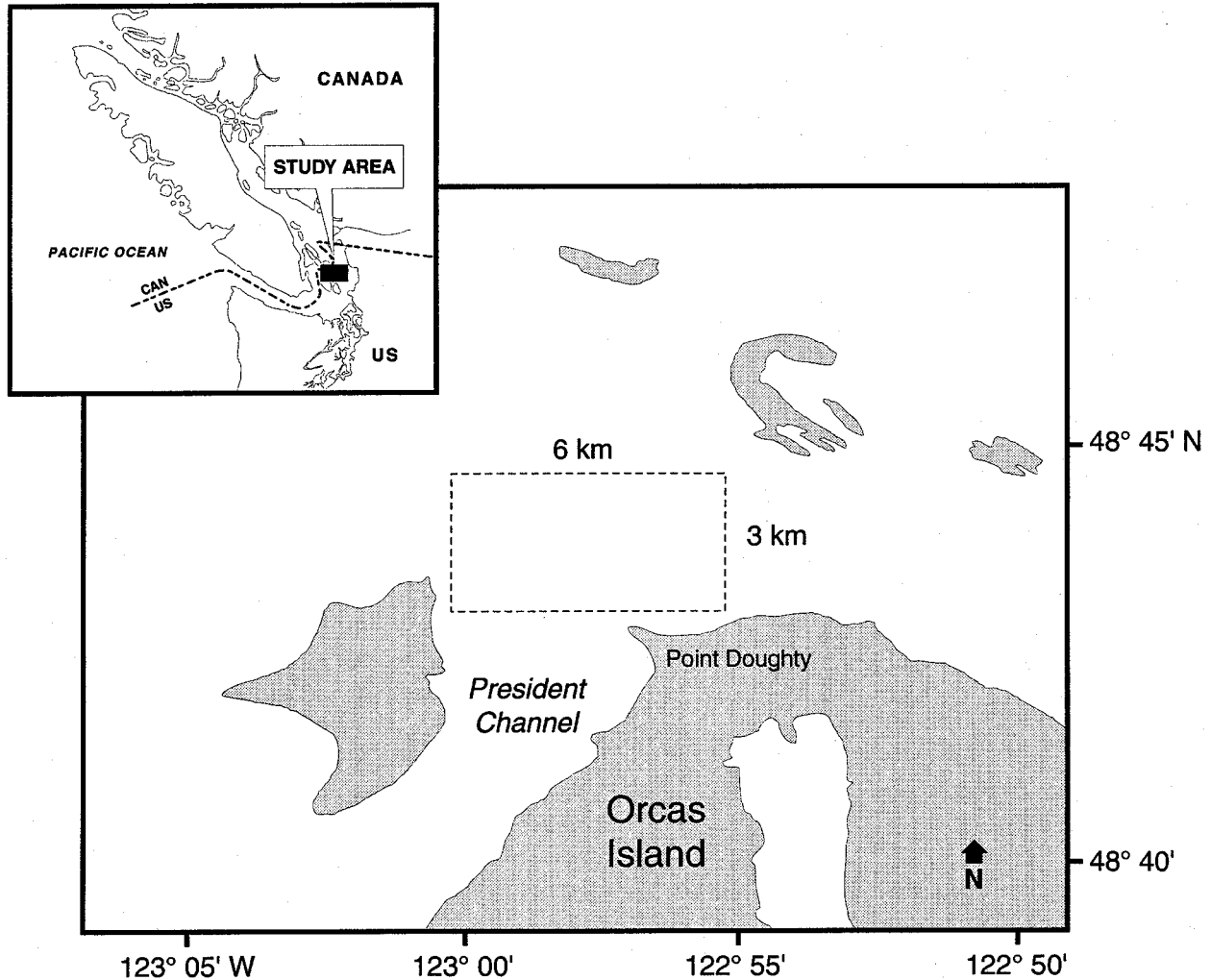


Fig. 1. Study area off the northwest side of Orcas Island in the San Juan Islands, Washington.

generally terminated when wind conditions exceeded 2 on the Beaufort scale (1% of sightings exceeded Beaufort 2), or when cloud cover was greater than 50% (11% of sightings exceeded 50% cloud cover). Perpendicular distance from the aerial transect line to a harbor porpoise group, $x_A = H \tan(90-\theta)$, was calculated from the aircraft altitude (H) and the angle (θ) between horizontal and the harbor porpoise group. The angle was measured with a clinometer when the group was abeam of the aircraft.

Position information was calibrated and tested in several ways. We calibrated the aircraft LORAN position at the study site using a known position on the runway. We determined the position of the land observation site by the average of LORAN positions from 17 aerial passes made on different days over the site. The deviation around this mean position ranged from 12 to 143 m and averaged 84 m ($SD = 34$). Accuracy

of the positions determined from the aircraft during transects was also determined from 50 passes over a research boat equipped with a GPS. The mean discrepancy between aircraft and boat positions was 91 m ($n = 50$, $SD = 60$) with 78% of the readings disagreeing by less than 125 m and 6% with discrepancies more than 200 m. These discrepancies may have been caused by: (1) the GPS position obtained from the boat; (2) error from the aircraft LORAN; (3) error in marking the time the aircraft passed the target; (4) error in determining the vertical angle to the sighting, and (5) deviations in aircraft course (i.e., crab angle) causing an incorrect estimate of when the target was perpendicular to the transect line.

Land-Based Observation Procedures

Two teams, consisting of 4–6 people each, made observations of harbor porpoise from land.

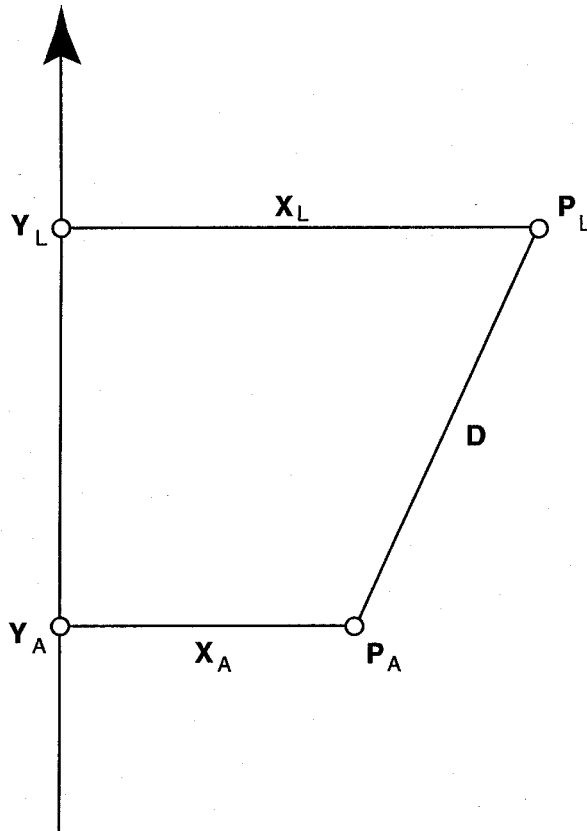


Fig. 2. Illustration of position and distance notation for land-based and aerial sightings of a harbor porpoise group relative to the aircraft transect line. Notations are defined in the text.

Each team attempted to track and obtain multiple position fixes on one group of harbor porpoise at a time. Harbor porpoise groups were tracked if they were far enough away from other groups to avoid ambiguity and if they were in the vicinity of the aerial transect lines. Each team consisted of: (1) at least 2 observers who used reticle/compass binoculars (7×50) to find and follow porpoise; (2) one person who obtained porpoise positions using an electronic theodolite (Leitz DT5 or Set-5), and (3) one person who recorded data with a computer linked to the theodolite to obtain horizontal and vertical angles. The data acquisition system computed a preliminary latitude and longitude in the field to ensure that the aircraft's route was near the harbor porpoise groups being tracked. The theodolite's elevation above the water, which varied with tide height, was measured directly with a plumb line (metric tape) every hour and was interpolated between the hourly readings during analysis.

Theodolites were calibrated daily by taking readings on 6 landmarks (4–8.5 km away). These readings were used to adjust the theodolite's

orientation to true north (determined in the field with a compass reading to a landmark) and to apply a fixed adjustment to the elevation above sea level. Theodolite positions of a boat equipped with GPS were 29–123 m from the recorded GPS position with a mean of 82 m ($n = 8$, $SD = 29$). In all cases the theodolite position was east of the GPS position. Some of this error may have stemmed from inherent error of commercially available GPS units created by selective availability (Herring 1996) or an inaccurate calibration of the GPS position to the U.S. Geodetic survey marker on Point Doughty where the theodolite was located.

$g(0)$ Experiments and Matching

An experiment for $g(0)$ estimation was a land-based sighting of a harbor porpoise group that was passed by the aircraft within a specific distance and time. For each land-based sighting, the time T_L and measured position P_L were recorded (Fig. 2). If the aircraft passed over a point Y_L such that the perpendicular distance x_L between Y_L and P_L was less than 200 m, and it did so at a time T_A within 240 seconds before or after the sighting from land ($T_P = |T_A - T_L| \leq 240$), the sighting was used in the analysis. The measured position P_A of harbor porpoise seen from the aircraft was computed from the recorded position Y_A and the perpendicular distance x_A . D was the distance between P_L and P_A , the measured positions of the land-based and aerial sightings.

The result of an experiment was either: (1) no aerial sightings of harbor porpoise during the pass; (2) an aerial sighting of a harbor porpoise group not seen from land, or (3) an aerial sighting of a harbor porpoise group tracked from land. Only the third result was considered a match (success). Aerial and land-based sightings were matched if the measured positions were sufficiently "close". We did not use harbor porpoise group size for matching because Calambokidis et al. (1993) demonstrated that land- and aerial-based estimates of group sizes were significantly different, suggesting that one or both were subject to bias.

Instead of choosing an arbitrary distance for determining a match, we constructed a model for the probability distribution of distance D between measured positions of land-based and aerial sightings of the same group. Measurement error for positions (P_L and P_A) and movement of harbor porpoise were modeled in the prob-

ability distribution of D (Appendix). Measurement error in x_A was small relative to errors in Y_A and was not included. We modeled measurement errors in latitude and longitude as independent normal distributions. We also assumed that errors in positions measured from land and air were independent with standard deviation σ_L and σ_A , respectively. These standard deviations were estimated from the repeated position measurements of the boat. We assumed that harbor porpoise movement was governed by Brownian motion (Ross 1983) in both latitude and longitude during a short time interval (<240 sec), which implies the changes in latitude and longitude of porpoise relative to their original position after a time interval T_p are each distributed as a normal with a mean of zero and a variance of $\sigma_m^2 T_p$. The expected value of the square of the distance moved is proportional to T_p , $E[d(T_p)^2] = 2\sigma_m^2 T_p$. An estimate of σ_m was computed from measurement of harbor porpoise movement observed from land at 1-minute intervals. One-half of the squared distance moved was regressed against the time between positions, with an assumed zero intercept. The slope provided an estimate of σ_m^2 . Based on the probability distribution of D for a specific value of T_p , the quantity D^* was computed such that D would likely only exceed D^* for 5% of the land-based and aerial sightings of the same group (Type I error, $\alpha = 0.05$).

Analysis Methods

The land-based and aerial observations provided 2 sources of data that we analyzed independently to examine visibility bias. The monitoring of surfacing intervals of 7 harbor porpoise groups from land provided an empirical estimate of availability, the proportion of time harbor porpoise are at, or near, the surface, and distributions of dive and surface interval lengths. The aerial $g(0)$ experiment, which determined whether the aircraft observers detected groups tracked from land, was analyzed based on a model of availability and perception. For model validation, the predictions of dive and surface intervals were compared to the empirical distributions, which were not used in the estimation of model parameters.

Surface and Dive Interval Data.—We monitored 7 harbor porpoise groups from land for extended periods of time and attempted to record each surfacing event. We were not able to distinguish individual porpoise, so we recorded

each surfacing of any porpoise in the group. The length of time harbor porpoise groups were at or near the surface was measured by combining all intervals with surfacings less than 30 seconds apart as a surface interval and longer intervals as dives. This approach, also used by Barlow et al. (1988), attempts to compensate for missing some surfacings within a series and for the horizontal perspective of the land-based observer that does not allow a full assessment of porpoise visibility from the aircraft. Surfacing were more likely to be missed in the first observed surface interval of a group of harbor porpoise, so it was excluded from the analysis of dive intervals for each group. We estimated average proportion of time spent at the surface and its standard error with a ratio estimator using each porpoise group as a sample (Cochran 1977:150–156).

Detection Probability Model.—The most obvious estimator for $g(0)$ is the proportion of harbor porpoise groups tracked from land that were seen by the aerial observers. However, it is unlikely that each harbor porpoise group had the same probability of being seen. Instead, we developed a model that describes the process of detection as a function of availability from diving and observer perception (i.e., detecting visible porpoise groups) and fitted the model to the observed successes and failures of the aerial observers in detecting harbor porpoise groups.

An aerial observer detects a harbor porpoise group when one or more porpoise are at or near the surface (availability) and the observer sees and recognizes the porpoise (perception). Many factors may affect whether porpoise at the surface are detected, but within the context of line transect sampling (Buckland et al. 1993), we explicitly recognize perpendicular distance x and consider all other factors as covariates \mathbf{Z} . We define perception at distance x as a conditional detection function $g(x|\mathbf{Z})$ to explicitly recognize that detection is conditional on the covariates \mathbf{Z} , and the event S that is the occurrence of one or more porpoise in a group at or near the surface within view. Availability is represented as $f(S,x)$, the probability that porpoise at perpendicular distance x are at the surface within the observer's field of view. It follows that the probability of detecting harbor porpoise at x , given covariates \mathbf{Z} , is:

$$g(x|\mathbf{Z}) = g(x|\mathbf{Z})f(S,x) \quad (1)$$

The standard assumption of line transect sam-

pling is $g(0) = 1$ (Buckland et al. 1993) which implies that $g(0|Z) = 1$ for all values of Z , and the effects of covariates are implicitly incorporated by their influence on the observed distances. We chose a logistic form to represent the probability an aerial observer saw a surfaced harbor porpoise group:

$$g(x|S, Z) = \frac{\exp(\beta_0 + \beta_1 x + \beta_2 z_1 + \dots + \beta_{r+2} z_r)}{1 + \exp(\beta_0 + \beta_1 x + \beta_2 z_1 + \dots + \beta_{r+2} z_r)}, \quad (2)$$

where z_1, \dots, z_r are possible covariates.

Availability, $f(S, x)$, will depend on the surfacing behavior of the porpoise and $w(x)$, the amount of time the ocean at perpendicular distance x is in the observer's view. Aircraft speed and how the observer scans the ocean will determine $w(x)$. McLaren (1961) devised a model for availability (see Eberhardt [1978] for a derivation) which assumes that observers view a semicircular area with fixed radius (r) forward of the observer, and animals are alternately unavailable and available for constant intervals of length d (dive) and s (surface), respectively. The probability that an animal is at the surface within the viewing area is the sum of the probability of being at the surface upon entering the viewing area [$s/(s+d)$] and the probability of being in a dive upon entry but surfacing within the viewing area:

$$\left[\frac{d}{s+d} \frac{w(x)}{d} \right]: f(S, x) = \frac{s}{s+d} + \frac{w(x)}{s+d},$$

and for McLaren's (1961) model

$$w(x) = \frac{\sqrt{r^2 - x^2}}{v}, \quad (3)$$

where v is aircraft velocity. Barlow et al. (1988) used a similar model for availability, but implicitly assumed the viewing area was square with length r , so $w(x) = r/v$.

We present an alternative model for availability by describing the surfacing and diving behavior of harbor porpoise as a 2-state continuous-time Markov process (Taylor and Karlin 1984). A surfacing interval is the period of time in which one or more porpoise in the group are at, or near, the surface during a series of shallow dives. A surfacing interval is followed by a dive interval, in which the porpoise are well below the surface and undetectable. A surface-dive interval is the period of time from the beginning

of one surfacing to the next. We assumed that the length of dive and surface intervals are independent exponential random variables with rate parameters λ and μ , respectively, and a surface-dive interval is the sum of the 2 independent exponential random variables. It follows that availability at perpendicular distance x is:

$$f(S, x) = \frac{\lambda}{\lambda + \mu} + \frac{\mu[1 - e^{-\lambda w(x)}]}{\lambda + \mu}. \quad (4)$$

Using the following equalities $E(d) = 1/\lambda$ and $E(s) = 1/\mu$, (4) can be re-written as:

$$f(S, x) = \frac{E(s)}{E(s) + E(d)} + \frac{E(d)[1 - e^{-\lambda w(x)}]}{E(s) + E(d)}.$$

If $\lambda w(x)$ is small, a first-order Taylor series approximation for availability is:

$$f(S, x) = \frac{E(s)}{E(s) + E(d)} + \frac{w(x)}{E(s) + E(d)}, \quad (5)$$

which is equivalent to McLaren's (1961) result, with constant values replaced by expectations. The approximation in (5) is valid for any non-negative distributions for dive and surface intervals. Using results from renewal theory (Ross 1983), availability is:

$$f(S, x) = \frac{E(s)}{E(s) + E(d)} + \left(\frac{\int_0^{w(x)} [1 - H(y)] dy}{E(s) + E(d)} \right), \quad (6)$$

where $H(\cdot)$ is the cumulative distribution function for dive intervals. If $w(x)$ is greater than any dive interval, the integral in (6) equals $E(d)$ and (6) yields the intuitive result that $f(S, x) = 1$. Using a second-order Taylor series approximation at zero for (6) yields the following approximation for availability:

$$f(S, x) = \frac{E(s)}{E(s) + E(d)} + \frac{w(x) - w(x)^2 h(0)/2}{E(s) + E(d)}. \quad (7)$$

For a first-order Taylor series, the approximation is equivalent to (5) and for dive distributions with $h(0)=0$, (7) is equivalent to (5). For the exponential distribution, $h(0) = \lambda$, but (7) is not substantially different than (5) for small values

of $\lambda w(x)$. McLaren's model is simply a special case for which dive and surface intervals are constant.

If we had known the locations of harbor porpoise groups (e.g., radiotagged animals) independent of being observed at the surface from land and had flown past them at various perpendicular distances, then we would have used (1) to represent the probability that an observer detected the group. However, we determined group locations by observing the surfacing of a group from land. Thus, our selection of groups was dependent on their temporary availability, and the probability that porpoise were at the surface for the aerial observers depended on T_p . Consider the extreme example of restricting $T_p < 1$ sec, which implies the plane passed by within one second of a land-based sighting. This restriction would almost surely guarantee that the group was still at the surface as the plane passed, effectively limiting the sample to available groups, and perception bias would be the only reason why groups were missed. This situation would be equivalent to flying a helicopter directly above a ship in the Buckland and Turnock (1992) approach, instead of out in front of the ship. Thus, the restriction on T_p influences the estimate unless the model for availability is appropriately stated conditional on T_p .

For the Markov process model of availability, the probability that porpoise are not at the surface at time t or $-t$, given that they are at the surface at time 0 (Taylor and Karlin 1984) is:

$$\begin{aligned} &Pr(\text{diving at time } t \text{ or } -t | \\ &\text{observed at the surface at time } 0) \\ &= \frac{\mu}{\lambda + \mu} [1 - e^{-(\lambda + \mu)|t|}]. \end{aligned}$$

Harbor porpoise are available if they surface at least once within the time an area is in view of the observer, which is the complement of being unavailable throughout the viewing time. Consider a land-based sighting of a group t seconds before the plane passes. This group is not available to be seen from the plane if it dives before $t - w(x)$ and remains beneath the surface until the plane passes. This occurs with probability:

$$\frac{\mu}{\lambda + \mu} [1 - e^{-(\lambda + \mu)(t - w(x))}] e^{-\lambda w(x)},$$

and the complement is the probability that it is available. In general, conditional on T_p , harbor porpoise are available with probability:

$$f(S, x | T_p) = 1 - \frac{\mu}{\lambda + \mu} \cdot [1 - e^{-(\lambda + \mu)t}] e^{-\lambda w(x)}, \quad (8)$$

where

$$t^* = \begin{cases} T_p & T_L \geq T_A \\ T_p - w(x) & T_L \leq T_A - w(x) \\ 0 & T_A - w(x) < T_L < T_A. \end{cases}$$

Strictly, (8) is conditional on both T_L and T_A to deal with the asymmetry created from assuming a viewing area forward of the observer; however, in aerial surveys the asymmetry is a minor consequence because $w(x)$ is small relative to the length of dive-surface intervals. Modifications of t^* will allow the viewing area to extend behind the observer.

Thus, we can represent the probability that aerial observers saw a harbor porpoise group, which was seen by the land-based observers at the surface, by the following simple modification of (1):

$$g(x | T_p, Z) = g(x | S, Z) f(S, x | T_p). \quad (9)$$

The n aerial experiments were assumed to be independent Bernoulli trials with probability p_i given by (9) which was dependent on the values of x , T_p , and Z for the i^{th} sighting. The realization for an experiment was $y_i = 1$ if seen and 0 if missed and the likelihood function was:

$$L(\lambda, \mu, \beta | y_1, \dots, y_n) = \prod_{i=1}^n p_i^{y_i} (1 - p_i)^{1 - y_i}. \quad (10)$$

Maximum likelihood estimates were obtained by solving numerically for the maximum of (10) with procedure NLMINB in SPLUS (Stat. Sci. 1993). We examined observer experience, group size (as estimated from land), Beaufort wind scale, and percent cloud cover as potential covariates in (2). Perpendicular distance as measured from land, x_L , was grouped into 2 100-m intervals, so x in (2) was treated as a factor with 2 levels. Distance was grouped to allow for error in distance measurement and change in the perpendicular distance between times T_L and T_A . The 100 m interval was chosen because the view of the observer looking through the belly window was limited to about 100 m on either side of the line. Side window observers could observe directly beneath the aircraft, but they typically concentrated beyond 100 m from the line. Our comparison of observers was limited to obser-

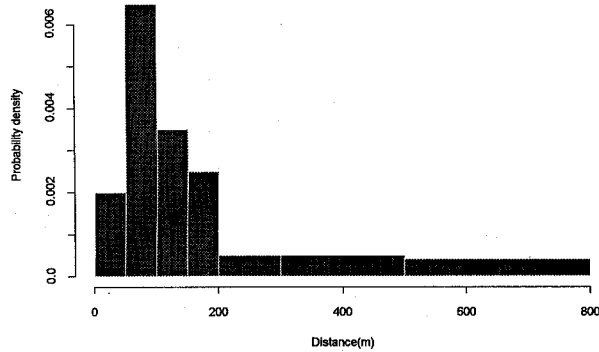


Fig. 3. Histogram of distance between land-based sightings and the closest aerial sighting for instances in which the aircraft passed the group's location within 50 seconds ($T_p \leq 50$) of being seen at the surface by the land-based observers.

vations within the first 0–100 m because inexperienced observers were only positioned at the belly window. We assumed $w(x)$ was represented by (3) with $r = 250$ m and used the average speed of 51 m/sec (100 knots) for v . Likelihood ratio tests with $\alpha = 0.05$ were used to assess significance of covariates.

Our primary interest was estimation of $g(0|\mathbf{Z})$ which is not conditional on the surfacing of a group at a point in time. An estimate of $g(0|\mathbf{Z})$ is given by (1) evaluated at 0, or as the limit of (9) as T_p approaches infinity, evaluated at 0. The limiting idea is analogous to finding a group from land at the surface and having a plane fly over at some random point of time in the future when the probability they are at the surface no longer depends on the initial surfacing. This independence is achieved in visibility experiments with radiomarked animals (Samuel et al. 1987) and can be partially achieved by separating the observations in time as in the helicopter-ship approach of Buckland and Turnock (1992). An approximate variance of $\hat{g}(0)$ was obtained via the delta method (Seber 1982).

RESULTS

Detection Probability Model

For the matching criterion, parameter estimates for measurement error were $\hat{\sigma}_A = 77.3$ m and $\hat{\sigma}_L = 62.0$ m. The regression of average harbor porpoise movement at 1–3 minute intervals ($R^2 = 0.42$, $n = 3$) provided an estimated standard deviation for movement between sightings t seconds apart of $\hat{\sigma}_m = 7.53$. When $T_p \leq 50$ sec, D^* ranged from 242 to 275 m, which appears to be reasonable when compared with the distribution of distances between land-based sightings and the closest aerial sighting (Fig. 3).

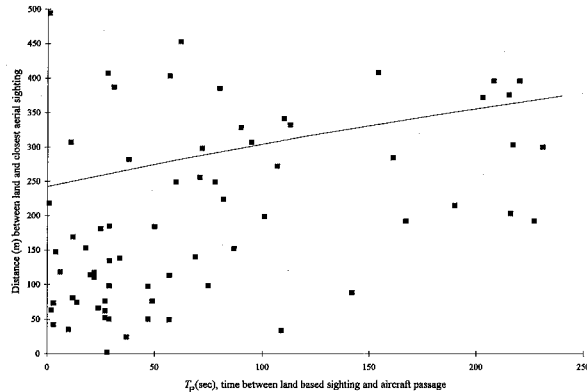


Fig. 4. Distance between a land-based sighting and the closest aerial sighting within 500 m during a pass, if any, for values of $T_p < 240$ seconds. The solid line is the distance criterion, D^* with $\hat{\sigma}_m = 7.53$. Groups below the solid line were treated as matches between land-based and aerial sightings.

The increase in average distance with increasing time between sightings is evident when the matching criterion is displayed as a function of time (Fig. 4). When $T_p > 150$ sec, all of the measured positions of aerial sightings were further than 200 m from the position of the land-based sighting.

Of all the land-based observations, 164 met the selection criteria, and of these 50 were seen by the aerial observers. Both distance and observer affected perception bias (Table 1). The only other significant covariate was T_p , which influenced availability of porpoise as represented by the surface-dive model (Table 2). The effect of T_p on detection probability is readily apparent (Fig. 5), and there was good agreement ($\chi^2 = 2.71$, 3 df, $P = 0.44$) between the observed and expected proportion of detections classified by T_p . The remaining factors, percent cloud cover ($P = 0.12$), Beaufort ($P = 0.89$), and group size ($P = 0.60$), were not significant.

Surface and Dive Intervals

Surface and dive times were obtained for 7 harbor porpoise groups (from 2 to 6 porpoise) that were observed consistently for 232 min (from 15 to 66 min/group). The average surface interval was 36 seconds, and the average dive interval was 127 seconds. The average proportion of time at the surface was 0.231 (SE = 0.032). Using the parameters λ and μ estimated from the detection probability model (Table 2), the predicted average surface time ($1/\mu$) was 58.1 seconds, and average dive time ($1/\lambda$) was 128.2 seconds. However, a likelihood ratio test of the null hypothesis that the model surface-

Table 1. Observed and expected number of aerial observations of harbor porpoise groups tracked from land, classified by experience level of the observer and distance interval as measured from land. The data are stratified based on the experience level of the observer stationed at the belly window. Inexperienced observers were not used at the side windows from which the 100–200 m interval can be viewed. Expected numbers seen and $\hat{g}(x|S, Z)$ (eq 2) were computed from the detection probability model with parameter estimates given in Table 2.

Observer	Position	Distance	<i>n</i>	# seen	$\hat{g}(x S)$	Expected
Experienced	Belly	0–100	58	29	0.86	29.8
Experienced	Side	100–200	44	10	0.47	10.2
Inexperienced	Belly	0–100	34	4	0.23	4.0
Experienced	Side	100–200	28	7	0.47	6.3

dive parameters were $\mu = 1/36$ and $\lambda = 1/127$ was not rejected ($\chi^2 = 2.52$, 2 df, $P = 0.28$).

***g*(0) Estimates**

Using the estimated model parameters with (4), our estimate of harbor porpoise availability at $x = 0$, $f(S, 0)$, was 0.338 (SE = 0.061). Using the empirical surface and dive interval data with (5), yielded an estimate of $f(S, 0) = 0.262$ (SE = 0.032). The probability an observer sees and correctly identifies a group that is near the surface within his/her field of view, $g(0|S)$, was dependent on the observer. For our experienced observers, $\hat{g}(0|S) = 0.865$ and $\hat{g}(0) = 0.292$ (SE = 0.107), and for our inexperienced observers, $\hat{g}(0|S) = 0.234$ and $\hat{g}(0) = 0.079$ (SE = 0.046).

DISCUSSION

Detection Probability Model

Availability poses a fairly significant problem in developing unbiased estimates of abundance because the necessary data are not easily collected during the survey in the manner that distances are used in distance sampling. With the exception of Schweder (1996), most double-observer (Palka 1995) or double-platform (Buckland and Turnock 1992) procedures for $g(0)$ estimation do not consider discrete availability of marine mammals. These capture-recapture (double-count) techniques are likely to over-estimate $g(0)$ (Schweder 1991a) unless there is sufficient separation in time (T_p) between the potential sightings by the observers or availability is incorporated through a model of surfacing behavior, as we have done here.

With a subsequent increase in computational complexity, our detection probability model and estimation procedure could be improved in several ways. A more general approach would model surfacing and diving as an alternating renewal process (Ross 1983) with possibly different distributions for surface and dive intervals. An ex-

ponential distribution for dive intervals is not entirely satisfying. The observed and predicted distribution of surface intervals agreed quite well (Fig. 6a), but more long surface-dive intervals were observed than predicted (Fig. 6b). The discrepancy may imply that the negative exponential predicts too many short dives but also partially reflects the inadequacies of observing surfacing behavior from land. The greater proportion of longer surface-dive intervals in the observed data could be partially explained by ignoring shorter dives that occurred between surfacings less than 30 seconds apart and by dives that were incorrectly lengthened because a surfacing was missed. However, the discrepancy is not critical because the effect of T_p was measured by conditioning on a surfacing event, and an exponential distribution provided an adequate fit for surface intervals (Fig. 6a).

A more complex model could also incorporate movement and measurement error into a probability distribution $\Phi(a \cdot a)$ for the position of a harbor porpoise group as a function of time from when the group was seen by the land-based

Table 2. Parameter estimates, standard errors, and deviance table for the detection probability model of aerial observations of harbor porpoise. For inexperienced observers within 0–100 m, $\hat{g}(x|S) = \exp(\beta_0)/(1 + \exp(\beta_0))$. For experienced observers, within 0–100 m, $\hat{g}(x|S) = \exp(\beta_0 + \beta_1)/(1 + \exp(\beta_0 + \beta_1))$, and within 100–200 m, $\hat{g}(x|S) = \exp(\beta_0 + \beta_2)/(1 + \exp(\beta_0 + \beta_2))$.

Parameter	Estimate	Standard error
λ -Dive	0.0078	0.0066
μ -Surface	0.0172	0.0107
β_0 -Intercept	-1.184	0.6664
β_1 -Observer	3.037	1.0490
β_2 -Distance	1.054	0.7340
Effect	df	Deviance
Surface-dive model	2	15.4
Observer	1	7.1
Distance	1	7.0
Residual	159	172.2
Total	163	201.7

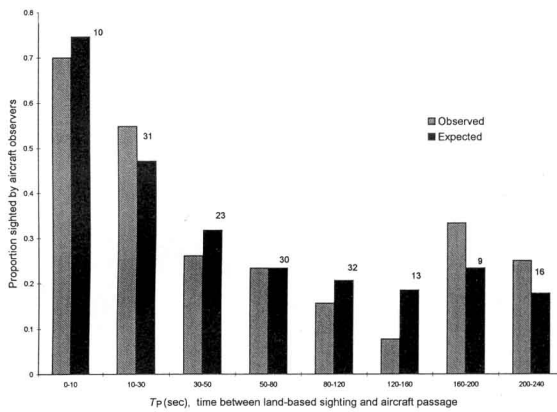


Fig. 5. Expected (predicted) and observed proportion of harbor porpoise groups sighted by the aircraft observers binned by values of T_p . The number of land-based sightings (experiments) is specified beside each bin.

observers. Including $\Phi(a \cdot a)$ into the likelihood would account for uncertainty in matching. Also, (9) could be written as an integral with respect to $\Phi(a \cdot a)$ to account for the uncertainty in the perpendicular distance, x , at the time the aircraft is in the vicinity of the group. Our estimates of $g(0)$ have used the perpendicular distance x_L at the time of the land-based sighting binned into 100 m intervals, because we do not know the exact location of the group at all times, unlike radiotagging experiments (Anderson and Lindzey 1996). We have assumed that detection probability is constant within the first 100 m and that harbor porpoise remain in the perpendicular distance bin until time T_A . Our estimates of $g(0)$ are negatively biased if either assumption is violated. A slight negative bias is suggested from the detection curve of Calambokidis et al. (1992), which predicted an average probability of detecting a surfaced harbor porpoise group within 100 m was 0.94.

The estimates of availability in the detection probability model depend on the assumption made regarding $w(x)$. Barlow et al. (1988) and Raum-Suryan (1995) have assumed that harbor porpoise are visible for 9 seconds at an average speed of $v = 160$ km/hour and $r = 400$ m. Although, harbor porpoise are visible at 400 m, the probability of detecting surfaced harbor porpoise at a perpendicular distance of 400 m was estimated to be less than 0.02 in the survey of Calambokidis et al. (1992). The definition of $w(x)$ illustrates the dependence between availability and perception in our model, because it is implicitly assumed that $g(x|S)$ is constant within $w(x)$ and zero outside. As $w(x)$ increases,

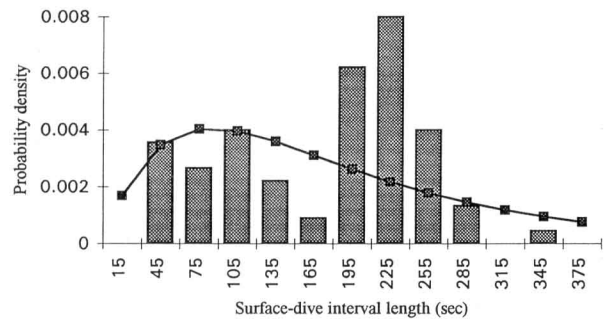
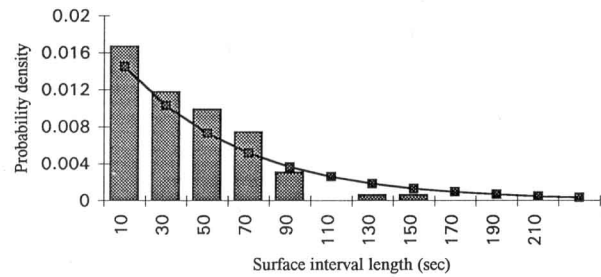


Fig. 6. Observed and predicted distributions of lengths of surface intervals (a) and surface-dive intervals (b). Observed distributions are histograms of the scaled frequency of interval lengths from monitoring 7 harbor porpoise groups with interval midpoints displayed on the axis. Predicted distributions are based on the surface-dive model with parameters estimated (Table 2) from the detection probability model.

apparent availability increases and $g(x|S)$ decreases. We chose $r = 250$ m because detection probability appears to decrease dramatically beyond that distance (Calambokidis et al. 1992). The assumed shape of $w(x)$ also affects the estimate of availability relative to perception. Our assumed semicircular viewing area, forward of the observer, implies a decrease in availability as x increases. A rectangular viewing area would have implied availability was constant for x . Any modeling of $w(x)$ and its relation to perception could be accomplished within the framework of an expanded hazard-rate model (Buckland et al. 1993:58–62; Schweder et al. 1996).

$g(0)$ Estimates

Availability bias is the primary source of visibility bias in aerial surveys of harbor porpoise. Both the model-based estimate of availability of 0.338 (SE = 0.061) and the empirical estimate of 0.262 (SE = 0.032), imply that assuming $g(0) = 1$ for line transect estimates of abundance will

produce substantial underestimates. Raum-Suryan (1995), using a boat, collected surfacing data for harbor porpoise at our study site for 2 summers. She estimated that harbor porpoise were at the surface 29% of the time, which would yield a comparable availability estimate of 0.318.

The empirical estimate of availability derived from land-based observations is based on a horizontal perspective and may underrepresent porpoise availability from the air because harbor porpoise can be seen beneath the water surface. But, the number of harbor porpoise seen beneath the surface will depend on factors that affect perception, such as sea state, sun glare, water clarity, cloud cover, and observer experience. During our experiment, sea state and cloud cover were not highly variable and were relatively ideal for viewing porpoise beneath the surface, which may have resulted in a higher estimate of availability from the aerial data. Also, our sampling procedure for land-based sightings may have been more likely to select groups with longer surfacing intervals because we would have been more likely to obtain a position with the theodolite.

For our experienced observers, it is likely that $g(0|S)$ is near unity when environmental conditions are ideal, and our model estimate of $g(0|S)$ is biased negatively by decreasing detection probability within the 0–100-m interval. However, the inexperienced observers were not nearly as successful in detecting available harbor porpoise. Our estimates suggest that these observers correctly detected fewer than one-fourth of the available harbor porpoise groups. Possibly, these observers were seeing some of the harbor porpoise groups but did not correctly identify them, or they were only detecting groups if one of the porpoise was above the water surface. The latter is supported by proximity of the percentage of groups that inexperienced observers saw, 7.9%, and the percentage of time that harbor porpoise are above the water surface, 7.2–7.5% (Watson and Gaskin 1983).

Clearly, there were differences between observers, but with our small sample of observers, it is less certain whether these differences resulted from experience or abilities. However, training through practice flights or pilot studies is important to help the observers develop a search image. If the aircraft has both a belly window and side windows, at least initially, inexperienced observers should be positioned at

the side windows until they become proficient. Fitting a detection curve to the observed distances will compensate for lack of proficiency if the inexperienced observer is stationed at the side window and an experienced observer is positioned at the belly window.

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APPENDIX

Distance Matching Criterion

An objective criterion was developed to determine whether positions of land-based and aerial sightings of a harbor porpoise group were of the same or different groups. The distance, D , between positions of land-based and aerial sightings of the same group is typically non-zero because of measurement error and movement of the group during the time between land-based and aerial sightings, T_p . We developed a simple statistical model of measurement error and porpoise movement and chose an upper limit D^* that was a function of T_p such that $\Pr(D > D^*) = 0.05$.

We assumed position measurements of aerial and land-based sightings were independent and unbiased but subject to independent, identically distributed normal errors in both latitude and longitude. We also assumed that harbor porpoise movement was governed by Brownian motion (Ross 1983) in both latitude and longitude during a short time interval (< 4 min). Given these assumptions:

$$\begin{aligned} P_L &\sim N(\mathbf{0}, \sigma_L^2 \mathbf{I}) \\ P_A &\sim N(\xi(T_p), \sigma_A^2 \mathbf{I}) \\ \xi(T_p) &\sim N(\mathbf{0}, \sigma_m^2 T_p \mathbf{I}) \end{aligned}$$

where $\xi(T_p)$ is the true position of harbor porpoise at T_A , and positions are relative to an origin at the true position of the harbor porpoise at time T_L . Let $K = D^2$ be the squared distance between the measured positions from land-based and aerial sightings. By definition, the cumulative distribution function of K is:

$$\begin{aligned} \Pr(K \leq \kappa | T_p) &= \int_{-\infty}^{\infty} \int_0^{\kappa} f_U(u | \xi(T_p)) N(\mathbf{0}, T_p \sigma_m^2 \mathbf{I}) du d\xi \\ & \hspace{15em} (A1) \end{aligned}$$

where the probability distribution $f_U(\kappa / (\sigma_A^2 + \sigma_L^2))$, conditional on $\xi(T_p)$, is non-central χ^2 with 2 degrees of freedom and non-centrality parameter λ (Graybill 1976:124-127):

$$\lambda = \frac{\xi'(T_p)\xi(T_p)}{\sigma_A^2 + \sigma_L^2}$$

We solved (A1) numerically for the 95% percentile, D^* , for several values of T_p between 0

and 240 second(s). From these values, we interpolated D^* for a specific T_p . Aerial and land-based sightings were considered a match if D did not exceed D^* .

DISTRIBUTION OF BLACK-TAILED JACKRABBIT HABITAT DETERMINED BY GIS IN SOUTHWESTERN IDAHO

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Abstract: We developed a multivariate description of black-tailed jackrabbit (*Lepus californicus*) habitat associations from Geographical Information Systems (GIS) signatures surrounding known jackrabbit locations in the Snake River Birds of Prey National Conservation Area (NCA), in southwestern Idaho. Habitat associations were determined for characteristics within a 1-km radius (approx home range size) of jackrabbits sighted on night spotlight surveys conducted from 1987 through 1995. Predictive habitat variables were number of shrub, agriculture, and hydrography cells, mean and standard deviation of shrub patch size, habitat richness, and a measure of spatial heterogeneity. In winter, jackrabbits used smaller and less variable sizes of shrub patches and areas of higher spatial heterogeneity when compared to summer observations ($P < 0.05$). During the low population phase, jackrabbits also used agricultural regions more during winter than summer. The association with agricultural regions was emphasized spatially in a GIS map contrasting winter and summer periods. Multivariate habitat means ($P < 0.001$), but not individual GIS variables ($P > 0.05$), differed significantly between high and low population phase. We used the Mahalanobis distance statistic to rank all 50-m cells in a 440,000-ha region relative to the multivariate mean habitat vector. On verification surveys to test predicted models, we sighted jackrabbits in areas ranked close to the mean habitat vector. Areas burned by large-scale fires between 1980 and 1992 or in an area repeatedly burned by military training activities had greater Mahalanobis distances from the mean habitat vector than unburned areas and were less likely to contain habitats used by jackrabbits.

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Key words: black-tailed jackrabbit, Geographical Information Systems, habitat ecology, *Lepus californicus*, landscape ecology, line transect, Mahalanobis distance, shrubsteppe, spatial habitat modeling, wildfire.

Black-tailed jackrabbits are important prey for raptors and other predators (Clark 1972, Johnson and Hansen 1979, Smith and Murphy 1979, MacCracken and Hansen 1987, Bates and Moretti 1994). In the NCA and surrounding region in southwestern Idaho, black-tailed jackrabbits and other abundant prey support one of the largest nesting densities of raptors in the world (U.S. Dep. Inter. 1979; Steenhof and Kochert 1985, 1988). A holistic approach is nec-

essary for management of ecological systems (Grumbine 1994). Therefore, managers should address nongame prey populations in land use planning to achieve often more visible goals, such as conservation of raptors, in a region.

The NCA, designated as a national conservation area (U.S. Public Law 103-64, 4 Aug 1994), also is used for livestock grazing, and military training. Wildfires are an additional disturbance to the habitat in the NCA and in recent years have fragmented shrublands and changed much of the landscape to exotic annual grasslands (Knick and Rotenberry 1995). In addition to temporal effects, land use and distur-

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