

DIEL VARIATION IN MIGRATION RATES OF EASTERN PACIFIC GRAY WHALES MEASURED WITH THERMAL IMAGING SENSORS

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ABSTRACT

We recorded the blows of gray whales during their southbound migration past central California in January 1994, 1995, and 1996, using thermal imaging sensors. For our sampling purposes, we defined day (0730–1630) and night (1630–0730) to coincide with the on/off effort periods of the visual counts being conducted concurrently. We pooled data across the three years of sampling and tested for diel variation in surfacing interval, pod size, offshore distance, migration rate, and swimming speed by comparing paired day/night means for samples collected within the respective 24-h period. We performed these tests using data from the entire migration period and then repeated the tests for samples collected prior to and after the approximate median migration date (15 January). Over the entire migration period we observed larger diurnal pod sizes ($\bar{x}_{\text{day}} = 1.75 \pm 0.280$, $\bar{x}_{\text{night}} = 1.63 \pm 0.232$) and greater diurnal offshore distances ($\bar{x}_{\text{day}} = 2.30 \pm 0.328$ km, $\bar{x}_{\text{night}} = 2.03 \pm 0.356$ km) but found no diel variation in surfacing interval. For the entire migration period, the nocturnal migration rate (average number of whales passing per hour) was higher than the diurnal rate. During the first half of the migration we detected no diel variation in pod size or surfacing interval, but diurnal offshore distances were larger than at night ($\bar{x}_{\text{day}} = 2.28$

± 0.273 km, $\bar{x}_{\text{night}} = 1.96 \pm 0.318$ km). Diurnal and nocturnal migration rates prior to 15 January were not different. During the second half of the migration, there was no diel variation in surfacing interval, pod size, or distance offshore, but the nocturnal migration rate was higher (28%, SE = 11.6%) than the diurnal rate. We found no diel variation in swimming speed in any comparison. We propose that later migrants socialize more during the day, which effectively slows their diurnal rate of migration relative to nocturnal rates.

Key words: cetacean, gray whale, *Eschrichtius robustus*, infrared, detection, migration, abundance estimation, thermal sensor.

Estimates of abundance for eastern Pacific gray whales (*Eschrichtius robustus*) have been based on various assumptions concerning the relationship between observed diurnal migration rates and unobserved nocturnal migration rates. Assumptions have been made that the nocturnal rate is slower (Gilmore 1960, Adams 1968), faster (Buckland *et al.* 1993; Hobbs *et al.*, in press), or the same (Reilly *et al.* 1980, 1983) when compared to the rate observed during daylight hours. Gilmore (1960) felt that gray whales may swim more slowly at night because they need to rest, require visual cues to navigate, or may feed at night. Hubbs and Hubbs (1967) observed that gray whales halt their evening migration during "the dark of the moon." In an effort to collect direct information on gray whale migratory behavior, Swartz *et al.* (1987a) attached radio tags to 20 southbound gray whales and tracked their movements both day and night. These authors concluded that there was no need to adjust shore-based estimates for diel differences in migration rates. However, a paired analysis of their data indicated that the rate of travel at night was greater (Buckland *et al.* 1993), with the results varying depending on the subset of the data used. If incorrect, the underlying assumption regarding nocturnal migration rate can cause the resulting abundance estimate to be positively or negatively biased if the nocturnal migration rate has been over- or underestimated, respectively. Furthermore, the fraction of survey time, for which visual observations cannot be made because of insufficient light levels, may comprise nearly two thirds of the survey duration (Rugh 1984; Hobbs *et al.*, in press). We sought to better quantify nocturnal migration rates and to determine if a correction factor for diel variation in migration rate should be considered when producing abundance estimates for this stock.

Researchers have tried to extend their shore-based survey effort into the evening using instruments that amplify ambient light. Reilly *et al.* (1980) reported that efforts to detect southbound gray whales from Granite Canyon with a starlight scope and night-vision goggles were largely unsuccessful, but the limited data they collected supported the hypothesis of no diel variation in migration rates. Rugh (1984) conducted an experiment using night-vision goggles to count southbound gray whales passing Unimak Island, Alaska, at dusk. Based on these observations during low-light periods, the diurnal and nocturnal sighting rates appeared equal in one test. However, an additional experiment conducted at night indicated that nocturnal sighting rates were

only 73% of diurnal rates. Overall, results of efforts to estimate migration rates with instruments that amplify available light have been inconclusive.

During the late 1960s and early 1970s, wildlife managers began to recognize the potential for using instruments that detect radiation in the far-infrared portion of the electromagnetic spectrum, also known as thermal radiation. The first studies showed promise (Croon *et al.* 1968, Graves *et al.* 1972), but it was not until the sensitivity of thermal imaging systems improved that these instruments began to equal or surpass traditional surveying techniques (Wiggers and Beckerman 1993, Sidle *et al.* 1993, Garner *et al.* 1995, Naugle *et al.* 1996). In the marine environment, thermal imaging systems have been used to study whales (Cuyler *et al.* 1992) and hauled-out pinnipeds (Barber *et al.* 1991; C. Duck, personal communication¹). Although Cuyler *et al.* (1992) showed that detecting whales through dermal temperature using these instruments appears unreliable, they found the thermal radiation emitted from a whale's blow differed from its surroundings by up to 4.0°C and provided a consistent positive signal. With technical support from the U.S. Army we tested a prototype military thermal imaging system from a bluff at a research station on the central coast of California to determine if the blows of migrating gray whales could be detected. Based on encouraging results from our 1993 field test, we conducted an experiment in the following three years to study diel variation in migration rates of eastern Pacific gray whales. Our objectives were to compare diurnal/nocturnal surfacing intervals, pod sizes, offshore distances, swimming speeds, and migration rates.

METHODS

We conducted our sampling from the Granite Canyon Research Station near Carmel, California. The National Marine Mammal Laboratory (NMML) has used this site for shore-based surveys of southbound migrating gray whales since 1975 (Reilly 1984). Our work was concurrent with NMML's gray whale surveys in January of 1994, 1995, and 1996. Each year we positioned the thermal sensors, which were mounted on tripods, approximately 25 m south of NMML's observation sheds and pointed the instruments perpendicular to the shoreline (about 241° magnetic). We used a single sensor during the 1994 field season, but in 1995 and 1996 we doubled our field of view by sampling simultaneously with two adjacent sensors.

The real-time thermal imaging system (the AN/KAS-1A) we used, which was loaned to us by the US Navy, focuses incoming thermal radiation of wavelengths from 8 to 12 μ onto a super-cooled array of sensors. The intensity of the radiation received by each sensor is converted into a pattern of voltages and then into an image that is recordable as video output. We recorded the output as standard black and white composite RS-170 video on two-hour VHS 120 video tapes. Data titlers inserted between the instruments and the video

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recorders provided time and date as part of the original data record. When we recorded data from two sensors, the clocks in the titlers were synchronized daily.

The AN/KAS-1A is designed to discriminate between objects that differ in temperature by as little as 0.1°C . It can be operated in a narrow ($1.1^{\circ} \times 2.2^{\circ}$, magnification $9\times$) or wide ($3.4^{\circ} \times 6.8^{\circ}$, magnification $3\times$) field of view. All of the samples collected for this experiment were taken in the wide field of view. Operating in this mode at a height of 22 m above sea level, the instrument could record data from the horizon to about 360 m offshore. The center of the gray whales' southbound migratory corridor was about 2 km offshore (Rugh *et al.* 1996), and at this distance a single sensor covered a horizontal area of roughly 240 m in the center of the field of view. Thus, it took a whale swimming at 5.6 km/h near the center of the corridor approximately 2.5 min to cross the sensor's field of view.

Because we sought to detect differences in migration rate that could bias estimates of abundance produced from shore-based visual counts, we defined day (0730–1630) and night (1630–0730) to coincide with the on- and off-watch periods of the visual survey. Each two-hour video tape was classified according to these definitions. In the few instances that a two-hour tape overlapped our established day/night boundaries, the tape was assigned to the period in which the majority of the two hours occurred (*e.g.*, a tape that sampled from 0700–0900 was assigned to the day period). Because the effectiveness of these instruments decreases in poor weather conditions (high winds, fog, or rain), our samples from each year were clustered into intervals of good weather (Fig. 1). In 1994 the weather was generally very good throughout January and our sampling regime consisted of four hours each day and night. In subsequent years, severe storms battered the central coast of California, and we conducted extensive sampling during the few periods of good weather.

Although we restricted our sampling to periods of good weather, the detection of blows varied within the range of weather conditions that we considered acceptable. For instance, during calm conditions with little or no wind, the blow of a whale appeared tall and columnar and remained distinctly visible for several seconds. As wind speed increased, blows became less distinct and were more easily lost in the clutter of small waves and white caps. Based on subjective criteria, we ranked the probability of detecting blows on each tape as follows:

Excellent—Calm seas, light wind, blows appearing as persistent columns.

Very good—Some small waves, light wind, blows less persistent but clearly visible.

Good—White caps visible, moderate wind, blows mixing rapidly and nearly horizontal, cues for blows sometimes confused with white caps, well-defined horizon.

Fair—Moderate seas and swells, blows horizontal and easily lost in confusion of sea surface, poorly defined horizon.

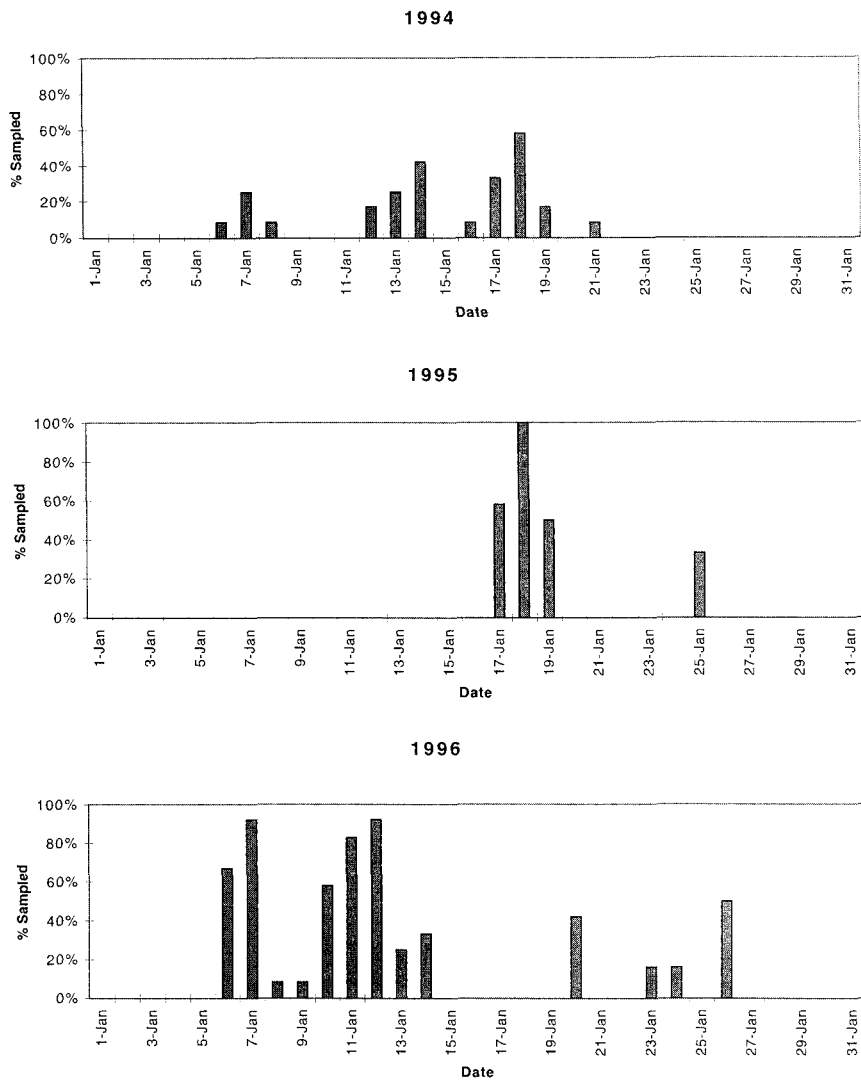


Figure 1. Thermal sensor sampling of southbound gray whales from Granite Canyon, California, in 1994, 1995, and 1996. Vertical bars represent percent of 24-h period during which data were collected in very good to excellent conditions.

Counting Procedures

We viewed each video tape at high speed, carefully reviewing sections with whales several times at slower speeds. To help track each whale within a pod, we attached acetate sheets to the monitor and marked each blow with colored pens. We defined pods as groups of whales swimming within two body lengths of one another. For each pod, we recorded the number of whales present and

the time of each surfacing. For each tape this process was repeated independently by at least two individuals. Pods missed by either individual were added to the final count. Differences in pod size estimation were resolved by reviewing the tapes and calculated surfacing intervals or, as a last resort, in favor of the more experienced interpreter. Because it was sometimes difficult to identify and track blows of individual whales within larger pods, we used only data from single whales (*i.e.*, pod size = 1) in our comparison of diurnal/nocturnal surfacing intervals and swimming speeds.

Distance and Speed Measurements

We calculated the distance offshore from the sensor to a whale by using the formula by Lerczak and Hobbs (1998), which uses the viewing height and the vertical angle between the horizon and a whale to compute distance. We determined the height of the sensors, 22 m above sea level, by measuring with a theodolite the height differential between the sensor and a nearby geodetic control reference mark (MIS GRAN RM#1, 1965) located within 20 m of the sensor. To measure the vertical angle, we imported the video images with whales into a computer using image-processing software and measured the distance in pixels from the base of the blow to the horizon. We converted this distance from pixels to degrees using a constant conversion factor ($0.0104^\circ/\text{pixel}$) calculated by measuring several objects of known length at known distances recorded by the infrared sensors.

We tested the accuracy of our calculated offshore distance measurements by using the infrared sensors to record a U.S. Coast Guard vessel as it occupied a series of positions at known distances from our survey site. Positions for the ship were determined on board using standard Global Positioning System (GPS) receivers. We measured the distance from the horizon to the waterline of the vessel and compared our calculated distances with those based on GPS data. We found a consistent negative bias in our calculated distances, which we corrected using linear regression analysis (1).

$$d_i = d * 1.122 - 0.042 \quad r^2 = 0.986 \quad (1)$$

where:

d = calculated distance (km)

d_i = true distance (km).

Using the same image-processing software described earlier, we measured the horizontal distances whales traveled across the monitor and used these measurements in conjunction with calculated offshore distances to determine swimming speeds. For each of these whales that surfaced at least twice, we measured the horizontal distance between the first and final surfacing. We converted this measurement from pixels to degrees as described above. We also calculated the offshore distance to each of these surfacings. Having calculated the corrected distance to the whale, we converted our angular mea-

surement in degrees to the horizontal distance traveled in kilometers using the approximation

$$b = 2d_i \cdot \tan(a/2) \quad (2)$$

where:

b = horizontal distance traveled (km)

d_i = corrected distance (km)

a = angular measurement (degrees).

We calculated the swimming speed over this distance by dividing the distance traveled by the time elapsed between blows. For some whales there were small differences between the offshore distance measurements of the first and final surfacings. In these instances, we used the average of the two offshore distances.

Analysis

As the southbound gray whale migration progresses through each season, both the rate of the migration and composition of the migrants (age and reproductive condition) change. Shore-based counts of southbound whales passing Granite Canyon increase steadily from early December, reach a peak around mid-January, and dwindle to insignificant numbers by the second week in February (Reilly 1984). Rice and Wolman (1971) found that near-term pregnant females are the first to migrate south and are followed by adult females who have recently ovulated, adult males, and finally immature animals. In order to minimize the effects of this changing composition on our results, we tested for diel differences in migration patterns by comparing paired samples collected within 24-h periods. For example, the average of the surfacing intervals collected during the day on 8 January would be paired with the average surfacing interval during the nocturnal hours of that same date. We tested for diurnal/nocturnal differences using paired t -tests for normally distributed data (surfacing interval, offshore distance, migration rate, swimming speed) and the non-parametric Wilcoxon test for comparisons of average pod size, the data for which are highly skewed because of the large number of single whales. For paired comparisons of diurnal/nocturnal migration patterns, we used only tapes with conditions rated either excellent or very good.

To assess diel variation in migration rate, we first had to address any potential changes in behavior between day and night that could bias our analysis; hence, we tested for diel variation in surfacing interval, group size, and offshore distance. If whales surfaced more frequently, traveled in larger groups, or swam closer to shore at night, their detection probability could be greater than that for whales recorded during the day. We also tested for diel variation in swimming speed, which could account for differences in observed migration rates between day and night. The data for all of these comparisons were recorded with a single sensor in 1994 and from two adjacent sensors during most of

the 1995 and 1996 field seasons. When two sensors were in operation, we included all group-size, offshore-distance, surfacing-interval, and swimming-speed data for the pods detected by the north sensor and added data for pods detected exclusively by the south sensor. Pods were linked across sensors by comparing the times, offshore distances, and locations of surfacings plotted on the acetate overlays. Surfacing-interval data were taken for all whales swimming alone that surfaced more than once within the field of view of either sensor. Thus, surfacing intervals of the same whale from both sensors were used. Any surfacing interval that spanned both sensors was not included. In 1995 and 1996 (the years during which two sensors were used), swimming-speed data were collected from single animals on the north sensor and data for single whales detected only on the south sensor added to this data set. In our analysis of migration rates, we used only data collected from the north sensor, in order to standardize effort across all three years of sampling. We conducted paired tests using data from the entire migration period and repeated the tests for the first and second halves of the migration, which were delineated by the midpoint of the migration (15 January).

In addition to these paired comparisons, we also used generalized linear modeling (GLM) with S-Plus (Venables and Ripley 1994) to examine the factors affecting migration rate and to test for diel variation in these factors. We used the data from each tape as a sample and used each "day" (here meaning a 24-h period) within a year as a block, in order to reduce the variability associated with changes in the migration rate and the unbalanced distribution of the data, which are clustered in periods of good weather. We used a negative binomial model (Venables and Ripley 1994) to cope with the overdispersion in the whale counts resulting from the whales traveling in pods. We examined tape rating (excellent to fair conditions), day/night time periods, and early/late migration periods as potential factors that could affect the counts. We used AIC (Sakamoto *et al.* 1986) to choose the most parsimonious model and likelihood ratio tests for significance testing.

RESULTS

Blows of southbound gray whales were clearly visible in the video output from the thermal sensors both day and night. Each year we detected whales at distances in excess of 4 km from our survey site, even out to 5.4 km in ideal conditions.

Surfacing Interval

Because the infrared sensor has a relatively narrow field of view, our average surfacing interval is negatively biased if the known duration of longer dives is taken into account. Our average surfacing interval (27 sec) is much shorter than the 102-sec average interval measured by Swartz *et al.* (1987b), which was based on a sample including longer dives. Our average surfacing interval (27 sec) is, however, identical to that found by Swartz *et al.* (1987b) for short

Table 1. Mean diurnal and nocturnal measurements for five factors studied during southbound migration of gray whales. Mean followed by one standard deviation, and sample size given in parentheses. For this experiment, day defined as 0730–1630 and night as 1630–0730. Whales per videotape was unit used to measure migration rate. Each videotape had two-hour duration. In 1995 severe weather precluded sampling during first half of migration (*i.e.*, prior to 15 January).

		Entire migration	First half of migration	Second half of migration
1994				
Surfacing interval (sec)	day	25.48 ± 10.18 (184)	26.07 ± 10.23 (84)	25.00 ± 10.17 (100)
	night	24.13 ± 9.1 (245)	24.75 ± 9.39 (105)	23.67 ± 8.89 (140)
Pod size (whales)	day	1.96 ± 1.4 (361)	1.85 ± 1.33 (156)	2.00 ± 1.46 (205)
	night	1.78 ± 1.25 (457)	1.77 ± 1.25 (203)	1.82 ± 1.27 (254)
Distance offshore (km)	day	2.49 ± 0.81 (237)	2.39 ± 0.77 (124)	2.59 ± 0.87 (113)
	night	2.09 ± 0.69 (353)	2.04 ± 0.75 (157)	2.13 ± 0.61 (196)
Swimming speed (km/h)	day	5.74 ± 1.02 (40)	5.90 ± 1.06 (20)	5.57 ± 0.98 (20)
	night	5.74 ± 1.22 (60)	6.20 ± 1.02 (24)	5.44 ± 1.26 (36)
Migration rate (whales per tape)	day	32.40 ± 16.66 (15)	28.75 ± 18.19 (8)	36.57 ± 14.95 (7)
	night	40.31 ± 16.41 (16)	31.38 ± 10.93 (8)	49.25 ± 16.59 (8)
1995				
Surfacing interval (sec)	day	25.33 ± 11.66 (156)	N/A	25.33 ± 11.66 (156)
	night	27.26 ± 14.12 (182)	N/A	27.26 ± 14.12 (182)
Pod size (whales)	day	1.78 ± 1.19 (348)	N/A	1.78 ± 1.19 (348)
	night	1.64 ± 1.11 (401)	N/A	1.64 ± 1.11 (401)
Distance offshore (km)	day	2.37 ± 0.67 (363)	N/A	2.37 ± 0.67 (363)
	night	2.30 ± 0.54 (329)	N/A	2.30 ± 0.54 (29)
Swimming speed (km/h)	day	6.20 ± 1.17 (47)	N/A	6.20 ± 1.17 (47)
	night	6.13 ± 1.06 (52)	N/A	6.13 ± 1.06 (52)
Migration rate (whales per tape)	day	22.13 ± 10.25 (15)	N/A	22.13 ± 10.25 (15)
	night	28.29 ± 8.44 (14)	N/A	28.29 ± 8.44 (14)

Table 1. Continued.

		Entire migration	First half of migration	Second half of migration
1996				
Surfacing interval (sec)	day	28.19 ± 19.43 (298)	27.94 ± 19.93 (236)	29.13 ± 17.54 (62)
	night	28.56 ± 19.24 (479)	28.09 ± 19.27 (419)	31.80 ± 18.84 (60)
Pod size (whales)	day	1.73 ± 1.14 (456)	1.69 ± 1.14 (320)	1.79 ± 1.17 (136)
	night	1.68 ± 1.2 (704)	1.72 ± 1.25 (574)	1.47 ± 0.95 (130)
Distance offshore (km)	day	2.13 ± 0.69 (432)	2.24 ± 0.70 (320)	1.78 ± 0.52 (112)
	night	1.87 ± 0.49 (700)	1.90 ± 0.50 (574)	1.70 ± 0.43 (126)
Swimming speed (km/h)	day	6.48 ± 1.42 (97)	6.46 ± 1.41 (78)	6.26 ± 1.50 (19)
	night	6.21 ± 1.50 (198)	6.26 ± 1.44 (172)	6.48 ± 1.91 (26)
Migration rate (whales per tape)	day	20.46 ± 9.50 (28)	21.76 ± 10.41 (21)	16.57 ± 4.61 (7)
	night	22.84 ± 10.56 (43)	23.36 ± 10.45 (36)	20.14 ± 11.57 (7)

Table 2. Results of two-tailed paired tests of diurnal/nocturnal means for five factors studied. Data were pooled for three years sampled. D = N indicates no statistically significant diel variation between means. Migration was divided into two halves based on median migration date (15 January).

	Entire migration	First half of migration	Second half of migration
Surfacing interval	D = N ($t = 0.29, P = 0.77, df = 23$)	D = N ($t = 0.44, P = 0.67, df = 12$)	D = N ($t = 0.23, P = 0.82, df = 9$)
Pod size	D > N ($Z = 2.22, P = 0.026, n = 23$)	D = N ($Z = 1.66, P = 0.10, n = 14$)	D = N ($Z = 1.60, P = 0.11, n = 9$)
Distance offshore	D > N ($t = 3.73, P = 0.001, df = 23$)	D > N ($t = 3.29, P = 0.005, df = 14$)	D = N ($t = 1.91, P = 0.093, df = 9$)
Swimming speed	D = N ($t = 0.14, P = 0.891, df = 18$)	D = N ($t = 0.03, P = 0.979, df = 9$)	D = N ($t = 0.27, P = 0.791, df = 8$)
Migration rate	D < N ($t = -2.63, P = 0.016, df = 20$)	D = N ($t = -0.05, P = 0.963, df = 10$)	D < N ($t = -3.74, P = 0.005, df = 9$)

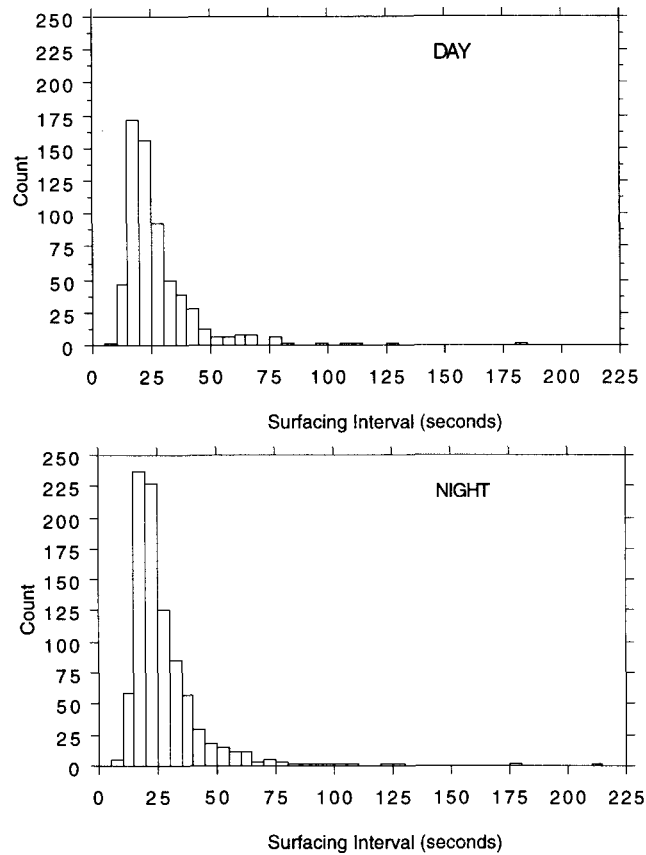


Figure 2. Surfacing intervals for all blows from single whales recorded with thermal sensors during day and night (1994–1996).

dives. Over the entire migration, average diurnal and nocturnal surfacing intervals (Table 1) did not differ ($t = 0.293$, $df = 23$, $P = 0.77$). Likewise, we detected no diel variation in average surfacing intervals in either the first or second half of the migration (Table 2).

Pod Size

The largest proportion of southbound pods consisted of single animals during both day (58% of all pods) and night (63%) (Fig. 3), and approximately one third of the total whales detected consisted of single animals (32% day, 37% night). Over the entire migration, average pod size was larger during the day (Wilcoxon paired-sample test, $Z = 2.22$, $n = 23$, $P = 0.026$). In both the first and second halves of the migration, the average pod sizes during the day and at night were not different (Table 2).

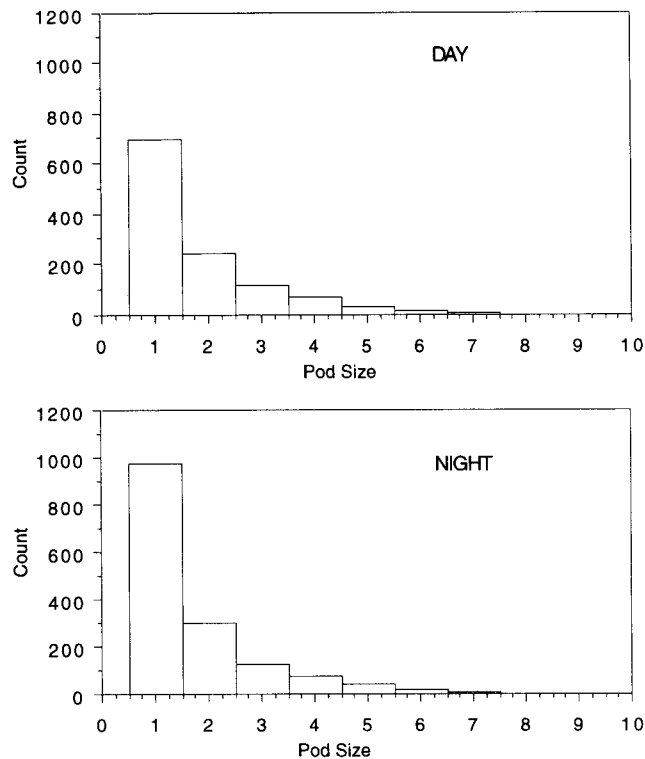


Figure 3. Frequencies of gray whale pod sizes detected by thermal sensors during day and night (1994–1996).

Distance Offshore

During the day, the center of the migratory corridor ranged from 2.5 km offshore in 1994 to 2.1 km in 1996 (Table 1, Fig. 4). The corridor was closer to shore at night for the entire migration period ($t = 3.73$, $df = 23$, $P = 0.001$) and during the first half of the migration ($t = 3.289$, $df = 14$, $P = 0.005$). During the second half of the migration, the mean distance offshore was not different between day and night ($t = 1.91$, $df = 8$, $P = 0.093$). Diel variation in average distance offshore was greatest (nearly 0.4 km) in 1994, when we experienced extended periods of light winds and calm seas.

Swimming Speed

The overall average swimming speed of southbound gray whales was 6.3 km/h for both day and night (Table 1, Fig. 5). We did not find diel differences in swimming speed over the entire migration or in either half (Table 2).

Migration Rate

When we compared diurnal and nocturnal migration rates recorded by a single sensor over the entire migration period, we found that the average

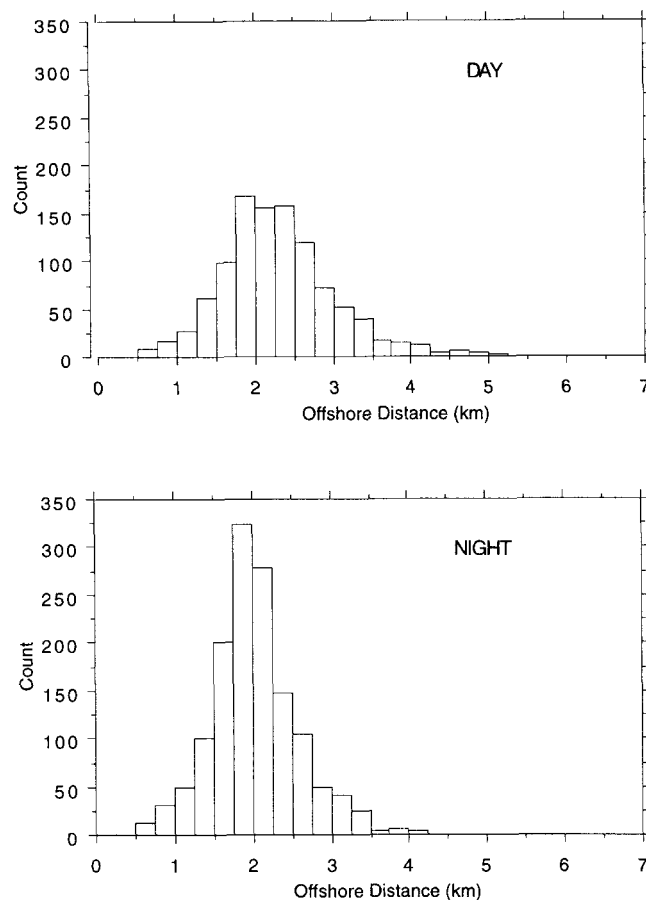


Figure 4. Histograms of distances to southbound gray whales passing Granite Canyon, California, measured from thermal sensor data during day and night (1994–1996).

number of whales per hour was higher at night ($t = -2.63$, $df = 20$, $P = 0.016$). The nocturnal migration rate during the second half of the migration was also higher than diurnal rate ($t = -3.78$, $df = 9$, $P = 0.005$). For the first half of the migration, our results indicated no diel variation in migration rate ($t = -0.05$, $df = 10$, $P = 0.96$). As expected, the GLM confirmed the results of the paired t -tests (Table 3). Both the “day” (meaning a 24-h period here) and condition ratings of the tapes were important determinants of the number of whales counted. The most parsimonious (lowest AIC) model also supported an interaction between day/night and migration period (first/second half) (Table 3). During the first half of the migration, the diurnal and nocturnal migration rates were not different, whereas the second half of the migration period showed a 28% higher (SE = 11.6%) nocturnal migration rate (Table 4).

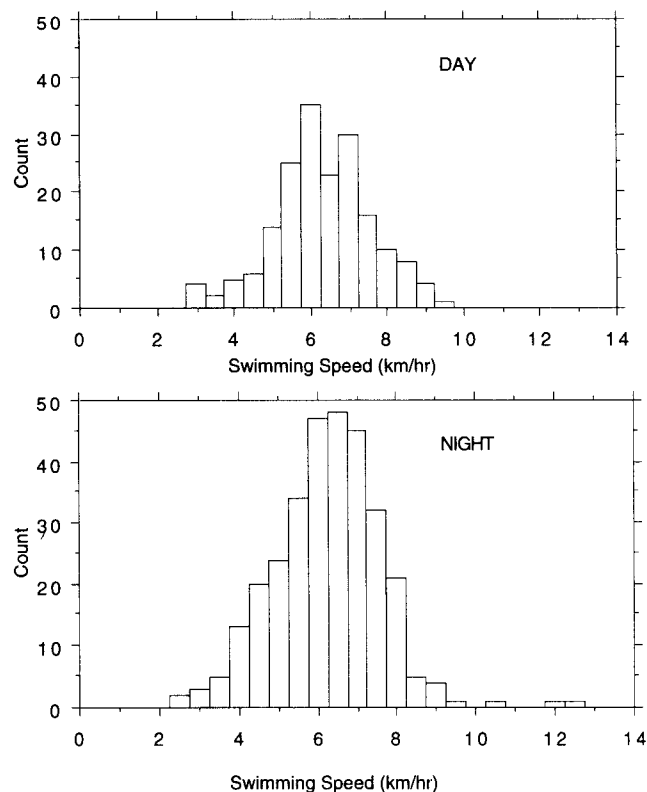


Figure 5. Swimming speeds calculated from thermal sensor data for single gray whales during day and night (1994–1996).

DISCUSSION

We began our analysis of the thermal sensor data by comparing diurnal *versus* nocturnal surfacing intervals, distances offshore, and pod sizes, because we surmised that large differences in any of these factors would bias our migration rate results. In the context of the entire migration period our results indicate that southbound gray whales swim farther offshore in larger groups during the day than at night. Nevertheless, we believe these differences would not affect our subsequent migration rate analysis, not only because the diurnal/nocturnal differences for pod size and distance offshore are very small, but also because they are inconsistent with the results of our tests for the first and second halves of the migration. In the case of offshore distance, for instance, we found no difference in migration rates during the period when the difference in diurnal and nocturnal offshore distance measurements was greatest. These tests indicated there was no diel variation in pod size in either the first or second half of the migration. Therefore, we eliminated pod size as a source that could bias our migration rate analysis. Only during the first half of the migration did whales swim farther offshore, and because diurnal and nocturnal

Table 3. Negative binomial GLM models fitted to set of counts from 2-h thermal sensor tapes collected in 1994, 1995, and 1996. Most parsimonious model (smallest AIC) boldface.

Model	Factors	No. of parameters	AIC	Likelihood ratio test (null: alternative)	P
0	None	1	-18,825		
1	Day/Year	34	-18,889	$\chi^2 = 130.6$	$P < 0.001$
2	Day/Year + Condition	37	-18,893	$\chi^2 = 10.3$	$P = 0.017$
3	Day/Year + DayNight	35	-18,891	$\chi^2 = 4.2$	$P = 0.041$
4	Day/Year + Condition + DayNight	38	-18,895	$\chi^2 = 3.0$	$P = 0.081$
5	Day/Year + Condition + DayNight : Period	39	-18,897	$\chi^2 = 7.3$	$P = 0.026$
6	Day/Year + Condition + DayNight : Period : Year	42	-18,891	$\chi^2 = 0.1$	$P = 0.987$

Table 4. Estimated coefficients and standard errors for tape condition and diurnal/nocturnal factors in negative binomial GLM. Coefficients parameterized relative to first level of factor (e.g., during second half of migration, expected nocturnal migration rate was $e^{0.246} = 1.28$ times expected diurnal rate; approximate standard error of multiplicative coefficient can be computed with delta method as $SE \approx 0.0908 * e^{0.246} = 0.116$).

Factor	Level	Coefficient	Standard error
Condition	Very good	+0.050	0.1059
	Good	-0.141	0.1389
	Fair	-0.525	0.2555
Diurnal/Nocturnal	≤ 15 January	-0.005	0.0817
	> 15 January	+0.246	0.0908

migration rates for this period were not different, declining visibility with increasing offshore distance does not provide a consistent explanation for the difference in migration rates. In addition, neither pod size nor distance offshore showed any diel variation during the late migration period, suggesting that diurnal and nocturnal detection probabilities for whales are similar. Yet, our nocturnal migration rate for this period was higher than the diurnal rate.

The different migration rate results for the early versus the late migration periods are consistent with the reanalysis Buckland *et al.* (1993) performed on the travel speeds (which included swimming and other behaviors such as milling or resting) measured through radio-tracking by Swartz *et al.* (1987a) and Swartz and Harvey (1985). Buckland *et al.* (1993) paired data for whales that were tracked both during the day and at night in their reanalysis in order to estimate a correction factor for nocturnal rate of travel. Prior to 15 January, six whales (five in 1986 and one in 1985) were tagged and monitored near Monterey. After 15 January, a total of nine whales were tagged and tracked, three near Monterey (all but one of them in 1986) and six in the California Channel Islands (all in 1986). A paired *t*-test we performed on these data demonstrated no diel variation in travel speed prior to 15 January ($t = -0.36$, $df = 5$, $P = 0.74$), whereas a difference in diurnal/nocturnal travel speeds occurred after this date ($t = 2.80$, $df = 8$, $P = 0.02$). Our results comparing migration rates between the first and second half of the migration showed this same pattern. Nevertheless, an equally valid comparison that stratifies the data by location rather than time period indicates diel variation in travel speeds for the whales tagged near the Channel Islands ($t = -2.73$, $df = 5$, $P = 0.04$) but no difference for whales tagged near Monterey ($t = -0.68$, $df = 8$, $P = 0.51$). Although time and area are confounded in this comparison, the early/late migration difference we detected is consistent with the data collected from the radio-tagged whales.

A higher nocturnal swimming speed could explain the higher nocturnal migration rates we observed, but we found no diel variation in swimming speed in any of our analyses. Thus, we hypothesize that the higher nocturnal migration rate detected after 15 January stems from the later migrants spend-

ing more time milling and socializing during the day. Rugh and Braham (1979) noted that the whales seen early in the southbound migration through Unimak Pass, Alaska, appeared to make fewer deviations from their southbound tracks than those passing later in the migration. They suggested that pregnant females, which make up a large proportion of the early migrants, may be more intent on reaching the calving lagoons, whereas later migrants may spend more time on social interactions. Although the results were only statistically significant in our entire migration period comparison, pod sizes were consistently higher during the day in all of our comparisons. This pattern may reflect an increase in social behavior during the day, which would support our proposed explanation for the higher nocturnal migration rate we observed.

Our results suggest that the current gray whale abundance calculations derived from the shore-based visual survey (Buckland *et al.* 1993; Hobbs *et al.*, in press) underestimate the population size. Both Buckland *et al.* (1993) and Hobbs *et al.* (in press) used a multiplicative correction factor of 1.02 to correct for nocturnal migration rates based on reanalysis of the radio-tag data of Swartz *et al.* (1987a). Based on our data, which show a 28% higher nocturnal migration rate for whales migrating after 15 January, the multiplicative correction factor for the entire visual survey based on a 15-h nocturnal (*i.e.*, non-survey) period would be $1 + 0.28f(15/24)$ or $1 + 0.175f$ [SE = $0.116 * (14/24)$] where f is the fraction of total whales migrating after 15 January. If 15 January is the median migration date, the multiplicative correction factor would be 1.09, which would imply current estimates of abundance for eastern Pacific gray whales should be increased by an additional 7%, or by approximately 1,400 whales.

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