Remote Estimation of Grey Seal Length, Width, and Body Mass from Aerial Photography

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Abstract

High-resolution images of two UK grey seal breeding colonies were derived from multi-temporal aerial photography and georeferenced in a GIS using ground control points obtained in the field with sub-meter DGPS. Lengths and widths of seals were digitized from these images. Elevations at seal locations were determined using sub-meter DEMs, allowing measurements to be adjusted for proximity to the camera. Mass estimates of seals were computed from these measures using models developed from direct field measurements. Comparisons of estimates derived from the images and actual masses of seals measured in the field indicate that this method provides a consistent index of relative body size. Seasonal patterns of changes in remotely determined size and mass estimates and inter-colony comparisons mirrored patterns observed from direct field measurements. Our work permits the remote estimation of seal body size for any sample of seals without the intrusive complications and sample limitations of direct field measurements.

Introduction

Phocid seals have been popular subjects for studies of breeding energetics because of their discrete breeding seasons, their uniform annual litter size, and their reliance on stored energy reserves for their breeding effort. Studies of the energetics of breeding grey seals (Anderson and Fedak, 1985; Anderson and Fedak, 1987a; Anderson and Fedak, 1987b; Fedak and Anderson, 1982; Fedak and Anderson, 1985; Twiss, 1991; Pomeroy *et al.*, 1999) have necessitated the capture and handling of individuals, which has several important limitations: (1) there is both an ethical and scientific need to minimize disturbance to the individual of interest and surrounding animals; (2) if energetics data are to be used alongside behavioral observations, it is necessary to prevent such activities from interfering with the natural behavior of the animals; (3) the aforementioned factors, together with the required field logistics of direct measurement, generally lead to relatively small sample sizes; and (4) there may be sampling biases due to differences in the probability of capture of individuals. Thus, a remote method of estimating energy expenditure would alleviate many of these problems.

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There has been considerable recent interest in methods of remote estimation of body mass for seals and sea lions. Various studies have demonstrated usable predictors of mass from morphometric measurements, taken in the field as either direct measurements (Castellini and Calkins, 1993) or by using conventional photography (Haley *et al.*, 1991). Data derived from remote mass estimates have subsequently been combined with behavioral data (Haley, 1994; Haley *et al.*, 1994). While this approach permits mass to be determined remotely for targeted individuals, it is less amenable for a large sample of individuals.

Aerial photography provides the potential to overcome these problems provided that the spatial grain is sufficient to resolve the shape of individual seals. Estep *et al.* (1994) demonstrated the use of image analysis of aerial photography and video footage for remotely measuring the length and breadth of harp (*Phoca groenlandica*) and hooded (*Cystophora cristata*) seals on pack-ice, a relatively flat, uniform platform. However, some species, such as the grey seal in the UK, breed on land where significant variation in the elevation at which seals breed can occur. Thus, application of such methods to grey seals would necessarily have to account for variation in elevation as this affects the proximity of individuals to the camera.

We used aerial photography to acquire relative indices of grey seal size by measuring the length and width of individuals. These measures were adjusted according the elevation at the individual's location as determined from high-resolution digital elevation models (DEMs). Estimates of mass were computed from these measures using models generated from direct field data. The accuracy of our method was tested by comparing these estimates with measurements made in the field. These remotely derived data are then used to examine intra- and inter-colony seasonal changes in length, width, and estimated mass for both male and female grey seals at two breeding colonies.

Background

The Grey Seal Breeding Season

Grey seals gather annually at remote, usually offshore, sites to breed. Breeding seasons extend over 8 to 10 weeks, each individual female being present for only 2 to 3 weeks, during which she gives birth to a single pup which she nurses for approximately 18 days, after which the pup is abruptly weaned and the female mates and departs from the colony (Anderson and

Photogrammetric Engineering & Remote Sensing
Vol. 66, No. 7, July 2000, pp. 859–866.

0099-1112/00/6607–859$3.00/0

Fedak, 1987a; Pomeroy *et al.*, 1994). Males remain ashore for varying lengths of time, depending upon their status (Anderson and Fedak, 1985; Twiss, 1991). During their stay in the colony, both females and males fast, relying on energy reserves stored primarily as the thick blubber layer. Lactating females lose weight at an average rate of 3.8 kg per day, males at 2.2 kg per day (Anderson and Fedak, 1987a; Anderson and Fedak, 1987b; Pomeroy *et al.*, 1999). Thus, not only is there a turnover of individuals during the season but each individual will lose mass and width during its stay. However, length should remain constant for an individual, and thus represent an independent measure of individual size, while mass and width provide information about the reserves which animals have stored.

Study Sites

Both of our study sites—North Rona (59°06′N, 05°50′W) and the Isle of May (56°11′N, 2°33′W)—are major UK grey seal breeding colonies. Elevation at these sites ranges from sea level to 50 m above mean sea level at North Rona and up to 21 m above mean sea level at the Isle of May.

Methods

Aerial Photographs

We used high-resolution color aerial photographs of our study sites taken at approximately 366 m altitude on 5- by 4-inch format film using a Linhoff Aerotechnika camera with a 150-mm lens. These aerial surveys are conducted annually by the Sea Mammal Research Unit (SMRU) for the purpose of estimating grey seal pup production (Hiby *et al.*, 1988). Photographs of North Rona and the Isle of May from the 1994 aerial survey were scanned onto Kodak Pro Photo-CDs at a resolution of 4096 by 6144 pixels. These images were then transferred in TIFF format to a GIS database (ARC-INFO Version 7.0.3): All images were registered and rectified to real world coordinates using ground control points (GCPs). Selected GCPs consisted of points located on permanent physical features identifiable both on the images and in the field. GCP locations were determined post-breeding season by use of a sub-meter accurate Carrier Phase Differential Global Positioning System (Magellan Nav 5000 Pro). Photo surveys of the Isle of May sites were available for four dates during the 1994 breeding season (17 and 28 October, 14 and 25 November), while those for North Rona were available for five dates (27 September; 08, 21, and 31 October; and 16 of November). For each date and site, a series of three or four images provided complete coverage of our study sites. Images were used (1) for measuring the length and width of seals and (2) for the generation of high resolution DEMs of the study sites. DEMs with a "sub-seal size" (approximately 2 m) resolution were required as part of a broader study of the topographical influences on grey seal breeding dispersion patterns (Pomeroy *et al.*, 2000; Twiss and Thomas, 1998). The full process used to generate DEMs has been described elsewhere (Mills *et al.*, 1997), but a brief summary follows.

The aerial photographs were not configured for DEM production because they were never intended for photogrammetric use. Photographs from a single survey date had a fore and aft overlap of no more than ten percent. However, as several flights were made over each colony during the course of a breeding season, several "opportunistic" overlaps, with typical base-to-height ratios of around 1:3, were available. With a Pro Photo-CD 64 base image giving a ground pixel size of 0.056 m, a best theoretical height RMS error of 0.17 m was expected.

Images making up the individual stereo pairs were typically taken several days apart, and this proved to be troublesome in the later stereo correlation due to seal movement and differing sea levels. Problems with varying lighting conditions between images were addressed by color balancing in Adobe Photoshop (Version 4.0), although heavy shadows on some of the images masked terrain detail. A further problem with the scans was that areas of interest on the diapositives had been marked by pin holes and red felt pen (Figure 1) for the purposes of counting pups prior to scanning. A mask was created for these areas, and the Photoshop "Replace Color" command was used to eliminate the lines where possible. The images were finally converted to greyscale and imported in TIFF format into the R-Wel Desktop Mapping System (DMS) (Version 4.0) low cost photogrammetric software.

A more serious problem with the use of Photo CD for photogrammetry was that approximately 7.5 percent of an image is lost from the edge during the scanning process (Thomas *et al.*, 1995) and, thus, there was no way of defining the image center and, hence, determining the principal point position on non-metric photography because the corners of the frame were lost. Using the corners of the scanned image to define the center was not possible because the photograph could move relative to the scanner between scans. Fortunately, the original diapositives were still available, and the positions of points that had been scanned on the Photo CD imagery were measured using a Zeiss Steko 1818 stereocomparator. The center of the image could then be extrapolated after measurement of the corresponding points on the scanned images in the DMS.

The non-metric camera used for the photography had never been calibrated and was unavailable for calibration. In an attempt to perform a calibration, eight Photo-CD images with varying degrees of kappa rotation of the Isle of May site were used, and 25 GCPs that had been observed in this area were measured on each. A bundle adjustment carried out on these eight images meant that a preliminary calibration of the camera was possible, and values for the interior orientation parameters were determined. The distortion determined in the lens was negligible (especially when considering that the Photo CD distortions were included in the adjustment), but values for the principal distance (149.873 mm) and principal point offset (+0.096 mm in the x axis and −0.819 mm in the y axis) were relevant and were utilized in later measurement.

The images were then orientated in the DMS using the

Figure 1. Grey scale version of part of a geo-rectified image from an aerial photograph of a grey seal breeding colony. The figure illustrates the image resolution and seals (white coat pups, which are approximately 1 m in length, can be clearly seen, with adjacent adult female seals, approximately 1.5 m in length). The red pen marks applied to the diapositives for the purposes of counting pups prior to the image scanning process are clearly visible as the dark grey streak running across the image.

derived interior orientation parameters together with the GCPs. Before the imagery was passed through the stereo correlation module, a mask was created over any water bodies that were not to be correlated. Differing sea levels on left and right images meant that the mask was created on the image with the highest sea level for individual stereopairs. The height of the masked area was attributed an elevation determined using the DMS's stereoplotting facility. Each stereopair was then passed through the stereo correlation module to produce the DEM. Input heights, that define the search range of the matrix in the x-parallax direction, were determined from the maximum and minimum GCP height values. Visual inspection showed the maximum 17 by 17 correlation matrix to give the best results (least number of obvious miscorrelations) for the 9-pixel (0.5-m) post DEM.

As expected, there were several large spikes present in the DEM due to miscorrelations resulting from problems associated with the different marks that had been made on the scans (some of which were still present despite use of the masking technique described earlier) and the presence of seals on the imagery. By passing a median filter with a high threshold value over the DEM, these effects could be eliminated, although inevitably the accuracy in some areas of high seal density was compromised. In an effort to assess the accuracy of the method, measurements to 15 GCPs on the Isle of May site were made, yielding an RMS error in height of 0.26 m (4.6 pixels). These had of course been used in controlling the images so could not be trusted implicitly to give a true accuracy assessment. Another survey was therefore needed which provided a higher order of accuracy to compare against. As the original diapositives were still available, it was decided to set up the same model in a Zeiss P3 analytical plotter and create a DEM of the area manually. Measurement in the P3 to the same 15 GCPs as measured in the DMS yielded a heighting RMS error of 0.13 m with a repeatability (precision) RMS error of 0.06 m. A 2-m grid of the area was then measured and compared against that from the DMS in the Land Survey System (LSS) ground modeling package. This enabled integrity of the P3 data to be maintained so that only interpolation on the surface produced by the DMS was required. The RMS error for the area was 0.47 m (8.4 pixels), with the DMS survey on average 1 pixel above that of the P3. This was attributed to the spikes that occurred due to miscorrelations. The accuracy across the DEM varied, with isolated areas of poor residuals found in the coastline areas and areas of high seal densities. RMS errors for ideal areas (away from both coastline and seal populations) were as low as 0.22 m (3.9 pixels), rising to 0.57 m (10.2 pixels) in the worst case areas. The value for the ideal case is only 1 pixel outside the theoretical best RMS error for DMS produced measurements, while the worst case is still within our original "sub-seal size" specification. Given the nature of the terrain and the amount of loose rock debris on the surface, this was deemed satisfactory. The DEM was exported in ASCII *xyz* format for inclusion in ARCINFO (Figure 2). DEMs were stored in the GIS as grid coverages representing elevation values, with a cell resolution of 0.2 m by 0.2 m. DEMs were resampled at a cell resolution of 2 m by 2 m, with cells values representing the mean elevation of the 100 original cells aggregated to form the lower resolution grids.

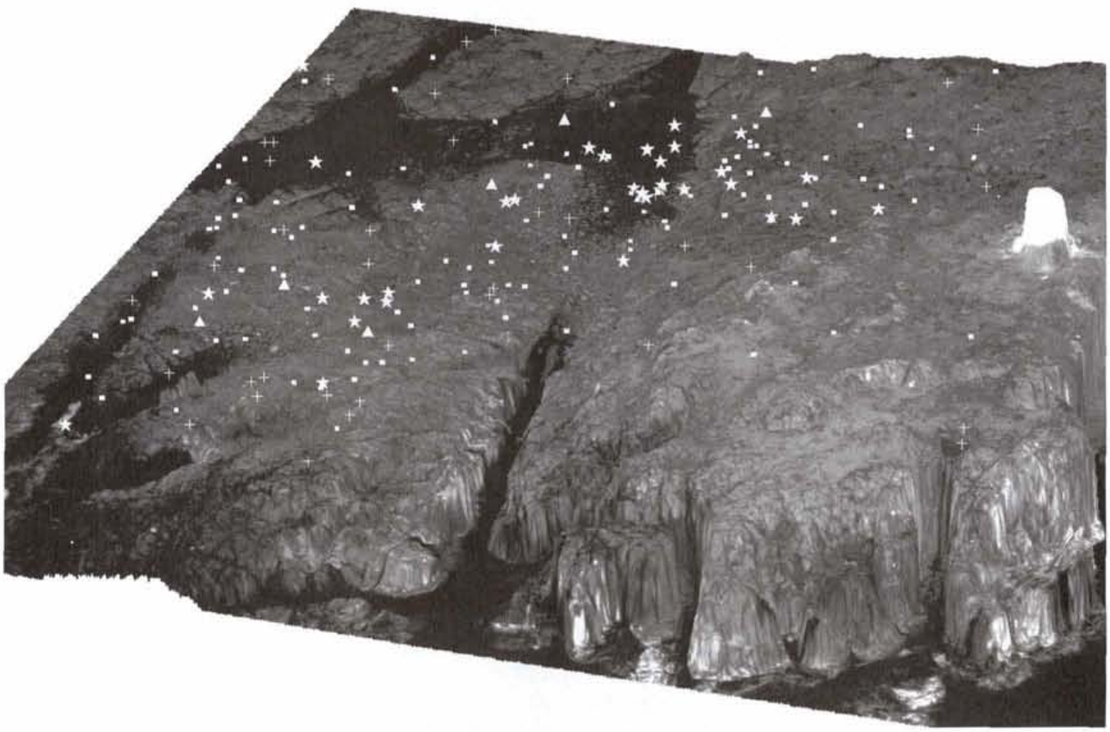

Figure 2. View of the Isle of May DEM with grey scale version of an image (derived from an aerial photograph taken from the 25 November 1994 survey) draped over the DEM. The white structure to the mid right of the image is a Fog Horn. A point coverage of seal locations from 25 November 1994 is draped over the DEM and image; ▲ = adult males, ★ = adult females, ▪ = white coat pups and + = weaned pups.

Measuring Seals from the Images

Seals were measured from geo-rectified images within the GIS rather than from ortho-rectified images. This is because seal locations and length and width measures were digitized prior to our development of the means of DEM extraction from the same images. As digitizing was extremely time consuming, it was deemed more appropriate for this study to use the method described above for adjusting measurements according to the elevation of seals locations. In addition, as DEM errors were worst in areas of higher seal densities, there was greater chance of areas of the images, and, therefore, seals, being distorted on an orthophotograph.

Using the rectified images as screen backdrops in ARCEDIT, the length and width of seals were digitized as straight 2D single arcs and stored as GIS coverages. We measured only those seals that were lying straight on relatively flat terrain and where the nose and posterior end of body were clearly visible. Each measured individual was classified as either adult male or adult female, both of which were easily distinguished from pups (Figure 1). Adult males were readily distinguished from adult females based on size, shape, and coloration. Males were larger and darker in color (generally dark brown to black) than adult females (generally grey) and of different shape, being relatively broader at the shoulders and narrower at the hip. Pregnant females were excluded from our analyses and were distinguished by their clearly bulging abdomens and tendency to group together in the absence of pups.

Length was measured from the tip of the nose of the seal to the posterior end of the main body mass, excluding the tail and hind flippers. Width was measured immediately behind the fore-flippers which is the widest part of the torso and where field measurements of axilliary girth are made. Thus, each seal measured was represented in the GIS coverages by two arcs and four nodes (start and end points of arcs). The x and y coordinates of the first node (the position of the nose) were used as point locations with which to sample the relevant DEM (at the 2-m cell resolution). Thus, accurate elevation values at the location of each measured seal's nose were obtained and combined in SPSS (version 7) data files with the relevant length and width measures (in meters), and date and site information. To account for differences in the proximity of individual seals to the camera, we adjusted the initial length and width measures according to the elevation at each seal's location using the formula

$$L_1 = L / [1/((-0.002734 \times E) + 1)]$$

where L_1 is the adjusted length (m), L is the initial measured length (m), and E is the elevation at the seal's location (meters above mean sea level). The -0.002734 value was derived from the slope of the regression of the linear increase in the apparent size of an object as it approaches a camera set at 365.76 m above mean sea level. The same equation was used for width measures, simply replacing length with width. Thus, we were able to adjust our estimates of length and width for errors induced by proximity to the camera.

Estimating Digitizing and Image Rectification Errors

Errors in our measurements from the images may derive from a number of sources: (1) inequalities incurred during the image rectification process, (2) camera elevation and angle varying between images, and (3) human error incurred in the digitizing process. At each site, rocks and other permanent features of similar size to seals (approximately 2 m) were measured on overlapping images from either the same or different dates. For each rock, three or four repeat measurements were made. Potential error was estimated very conservatively as the range in values obtained for each rock expressed as a percentage of the smallest of the replicate measures. For each study colony, 30 rocks were measured. Average error values were 2.7 percent for the Isle of May and 3.4 percent for North Rona.

Generating Models for Estimating Mass from Field Measures of Length and Width

Regression models predicting mass from length and width measures were derived from 239 seals that were directly measured in the field on 730 occasions. These data were from adult male and female grey seals captured during the breeding season on North Rona between the years 1987 to 1989 and from adult females on the Isle of May between 1988 and 1990. All females were post-partum. Details of the immobilization and weighing of adult grey seals can be found in Anderson and Fedak (1985) and Twiss (1991). Measurements of straight line nose-to-tail length and axilliary girth (immediately behind the fore-flippers) were taken from all captured seals. All possible attempts were made to ensure that each seal was lying on its ventral surface in a straight line, to minimize measurement errors. Weighings were accurate to $\pm$ 0.5 kg. These standard measurements were used to establish separate models for estimating the mass of females and males. Our aim was to generate robust models, based on parameters that could be determined from the aerial photographs; specifically length, width, and date during the breeding season. That is, models that exclude individual identity, as it was impossible to identify specific individuals from the aerial photographs.

Statistical Comparisons of Remotely Derived Measurements

Intra- and inter-colony seasonal changes for both females and males were examined using the following variables determined from the images: (1) width (cm), (2) length (cm), (3) estimated mass in kg (log10 transformed), and (4) the ratio of mass to length, a measure of the relative body condition of individuals. As the timing of the breeding seasons differs for the two colonies, with the North Rona season commencing earlier, dates in all analyses are expressed relative to peak pupping date for each site (North Rona peak pupping date = 29 September, Isle of May = 19 October). Peak pupping dates (day 0) were defined as the date on which the maximum rate of change in pup numbers was observed graphically from plots of white coat pup numbers through the season at each site. Pupping curves conform reasonably to normal curves (Coulson and Hickling, 1964), at least during the rising phase of pup numbers, the period in which peak pupping occurs. As each individual seal loses mass during their stay on the breeding colony, it is likely that individual identity may be important in estimating mass, especially if some individuals are present in images from more than one date. Therefore, for our intra- and inter-site comparisons of the remotely derived measurements, we split the data into early and late season periods. These broad temporal categories reduce the likelihood of the same individuals being present in both periods while permitting intra-seasonal changes to be explored. We use peak estrus date as the cut-off point for classifying data as either early (pre-peak estrus) or late season (post-peak estrus). Peak estrus date was defined as peak pupping date plus 19 days (the approximate time from parturition to entering estrus; Bonner, 1972), i.e., day 19. This represents the date on which the maximal number of females are likely to be in estrus. All datasets were examined for normality and were transformed where appropriate. Comparisons between sites and between early and late periods of the breeding season (see below) were by t-test. No statistical comparisons were made between sexes, because grey seals are sexually size dimorphic. Note also that the sample sizes of males (Table 3) for the Isle of May are considerably less than at North Rona. This is due to the Isle of May study site covering a smaller area and a more skewed operational sex ratio on this

Table 1. Summaries of the Regression Models Derived from Actual Field Measurements for Females (a) and Males (b). These models use the Volume of the Seal (V). This Was Estimated Using a Crude Cylindrical Model ($\pi r^2 h$ Where r is the Radius of the Axilliary Girth (Assumed to Be Circular) and h is the Nose-to-Tail Length). Note: Volume in cm^3, Radius in cm, and Date Measured in Days Relative to Peak Pupping Date (North Rona Peak Pupping Date = 29 September, Isle of May = 19 October).

(a) Females:
log 10 (actual mass) = $-2.75 + (1.016 \times \log 10(V)) - (0.000584 \times \text{date}) - (0.419 \times \log 10(r)$
Adjusted $R^2 = 0.841$, $F_{3,521} = 927.59$, sig. F < 0.0001

Variables in the Equation	Adjusted R^2	F Change	Sig. F Change
Log 10 (V)	0.836	2665.162	< 0.001
Date	0.839	12.411	< 0.001
Log 10 (r)	0.841	8.380	0.004
Variables not in the equation		Animal ID, nose-to-tail length	

(b). Males:
log 10 (actual mass) = $-2.56 + (1.120 \times \log 10(V)) - (0.000874 \times \text{date}) - (0.938 \times \log 10(r)$
Adjusted $R^2 = 0.849$, $F_{3,201} = 383.61$, sig. F < 0.0001

Variables in the Equation	Adjusted R^2	F Change	Sig. F Change
Log 10 (V)	0.827	978.974	< 0.001
Date	0.839	15.184	< 0.001
Log 10 (r)	0.849	14.941	< 0.001
Variables not in the equation		Animal ID, nose-to-tail length	

colony, approximately one male to ten females, compared to one to six at North Rona.

Results

Models for Estimating Mass from Length and Width Measures

Separate regression models for females and males were constructed from direct field measurements of seals with actual mass (log transformed) as the dependent variable and length, width, cylindrical volume (using length and axilliary girth measures), date during the season (measured as number of days relative to peak pupping date), and animal identity as independent variables. Unlike during direct field measurements, individual animal identities cannot be determined from the images; therefore, only models based on direct field measurements which excluded animal identity were selected for use with the remotely measured lengths and widths. Those models which excluded animal identity and provided the maximal adjusted R^2 values for each sex are presented in Table 1.

Remote Measurements from Images: Intra- and Inter-Site Comparisons

The respective model was used to estimate mass for female and male seals measured from the images. Data were divided into values from the early season period and the late season period. Within-site comparisons of values for the four variables between early and late periods (Table 2) indicate that Isle of May females show a significant decline in all four variables from early to late periods. Isle of May males showed significant reductions in length, mass, and mass-to-length ratio, but no significant change in width over the same period (Table 2). North Rona males and females also showed a reduction in estimated mass and mass-to-length ratio from the early to the late part of the season (Table 2). Unlike the Isle of May seals, neither male nor female lengths differed between early and late season at North Rona. However, both sexes did show a reduction in width. Inter-site comparisons for the early season period (Table 3) revealed that Isle of May females were significantly longer but thinner than those at North Rona, and consequently showed lower mass-to-length ratios. However, there was no difference between sites in estimated mass for females during this early period. In the late season period (Table 3), Isle of May females remained thinner than their counterparts at North Rona, but there was no significant difference in length between sites. Isle of May females showed lower estimated mass and mass-to-length ratios than did North Rona females in this later period. During the early season period, Isle of May males were longer than North Rona males, but no difference in length was found in the late season period (Table 3). They were also slightly thinner ($0.01 < p < 0.05$) than males at North Rona in both early and late season periods. Estimated mass showed no significant difference between sites for the early period; however, in the late season period, Isle of May males had slightly lower masses than did North Rona males, though not significantly so ($0.01 < p < 0.05$). However, mass-to-length ratios were significantly different between sites, with Isle of May males having lower ratios in both early and late periods.

Discussion

The Use of Aerial Photography for Remotely Assessing Seal Sizes and Estimating Masses

Remote measurement of seals from aerial photography suffers from imprecise knowledge of the distance from the camera to the seal caused by variations in flying height and the elevation of the seal (particularly where terrain varies considerably). The technique described here addresses these two major sources of error: (1) the use of very accurate GCPs for geo-referencing and image rectification in conjunction with the high resolution of the scanned images minimized errors due to variations in flying height, and (2) by using highly accurate DEMs of these study sites, we were able to eliminate potential errors caused by differences in elevation of seal locations. Thus, we were able to measure length and width of seals in real world units directly from the aerial photographs. Using field measurements of seals, we have developed robust models for estimating female and male mass from the measurements taken from the aerial photographs.

It is difficult to compare our original field data directly with values determined from the aerial images due to the differing time of season in which each were collected. However, we can compare seasonal averages from both datasets. Mean values for width measured from the images tended to be 2 to 5 cm (approximately 10 percent) greater than the widths of seals measured in the field. Field measurements were of axilliary girth, and width was estimated as the radius of girth, assumed to be a circle. As it is likely that the true cross section of a seal is slightly elliptical, we would expect measurements from above a seal to be slightly greater. Our length determinations from the images were between 17 and 27 cm shorter (approximately 10 to 15 percent) than those taken in the field. Field measurements

TABLE 2. COMPARISONS BETWEEN EARLY AND LATE SEASON PERIODS OF REMOTELY DETERMINED WIDTH (cm), LENGTH (cm), ESTIMATED MASS (KG), AND MASS TO LENGTH RATIO FOR (a) ISLE OF MAY FEMALES, (b) ISLE OF MAY MALES, (c) NORTH RONA FEMALES, AND (d) NORTH RONA MALES. NOTE: (1) EARLY = PEAK PUPPING DATE OF 0 OR LESS, LATE = PEAK PUPPING DATE GREATER THAN 0; (2) WHEN VARIANCES ARE UNEQUAL (TESTED USING LEVENE'S TEST FOR EQUALITY OF VARIANCES, $P < 0.05$), SIGNIFICANCE, DEGREES OF FREEDOM (d.f.), AND T-VALUES ARE TAKEN FROM T-TEST FOR UNEQUAL VARIANCES (HENCE, d.f. < $\Sigma n - 2$); (3) FOR ESTIMATED MASS AND MASS TO LENGTH RATIOS, THE MEAN AND STANDARD ERRORS (s.e.) PROVIDED ARE FROM UNTRANSFORMED DATA, HOWEVER, T-TESTS WERE CONDUCTED ON LOG10-TRANSFORMED DATA WITH THE EXCEPTION OF TESTS APPLIED TO THE ISLE OF MAY MALES; AND (4) POSITIVE T-VALUES INDICATE GREATER MEAN VALUES FOR THE EARLY SEASON PERIOD.

(a) Isle of May Females:	mean (s.e.) early (n = 202)	mean (s.e.) late (n = 237)	d.f.	t-value	sig.
Width	47.8 (0.5)	44.1 (0.4)	408.2	6.11	<0.001
Length	145.5 (0.9)	139.2 (0.7)	396.4	6.53	<0.001
Estimated mass	152.4 (3.0)	123.1 (2.1)	437	8.05	<0.001
Mass:Length ratio	1.03 (0.02)	0.88 (0.01)	437	7.32	<0.001
(b) Isle of May Males:	**mean (s.e.) early (n = 19)**	**mean (s.e.) late (n = 22)**	**d.f.**	**t-value**	**sig.**
Width	52.6 (1.1)	49.6 (1.3)	39	1.75	0.087
Length	189.1 (1.8)	174.9 (3.4)	31.6	3.67	0.001
Estimated mass	246.6 (8.5)	200.4 (10.0)	39	3.45	0.001
Mass:Length ratio	1.30 (0.04)	1.14 (0.04)	39	3.02	0.004
(c) North Rona Females:	**mean (s.e.) early (n = 219)**	**mean (s.e.) late (n = 371)**	**d.f.**	**t-value**	**sig.**
Width	49.5 (0.4)	47.7 (0.3)	588	3.32	0.001
Length	139.4 (0.9)	139.4 (0.7)	588	0.05	0.958
Estimated mass	152.3 (2.5)	140.0 (2.1)	512.4	4.22	<0.001
Mass:Length ratio	1.09 (0.01)	0.99 (0.01)	505.1	5.31	<0.001
(d) North Rona Males:	**mean (s.e.) early (n = 96)**	**mean (s.e.) late (n = 93)**	**d.f.**	**t-value**	**sig.**
Width	56.2 (0.7)	53.13 (0.6)	187	3.38	0.001
Length	174.6 (1.4)	174.9 (1.5)	187	−0.15	0.879
Estimated mass	248.1 (5.7)	218.8 (4.9)	187	4.03	<0.001
Mass:Length ratio	1.41 (0.02)	1.24 (0.02)	187	5.54	<0.001

TABLE 3. COMPARISONS BETWEEN SITES OF REMOTELY DETERMINED WIDTH (cm), LENGTH (cm), ESTIMATED MASS (KG), AND MASS TO LENGTH RATIO FOR (a) EARLY SEASON FEMALES, (b) LATE SEASON FEMALES, (c) EARLY SEASON MALES, AND (d) LATE SEASON MALES. NOTE: (1) EARLY = PEAK PUPPING DATE OF 0 OR LESS, LATE = PEAK PUPPING DATE GREATER THAN 0; (2) WHEN VARIANCES ARE UUNEQUAL (TESTED USING LEVENE'S TEST FOR EQUALITY OF VARIANCES, $P < 0.05$), SIGNIFICANCE, DEGREES OF FREEDOM (d.f.), AND T-VALUES ARE TAKEN FROM T-TEST FOR UNEQUAL VARIANCES (HENCE, d.f. < $\Sigma n - 2$); (3) FOR ESTIMATED MASS AND MASS TO LENGTH RATIOS, THE MEAN AND STANDARD ERRORS (s.e.) PROVIDED ARE FROM UNTRANSFORMED DATA: HOWEVER, T-TESTS WERE CONDUCTED ON LOG 10 TRANSFORMED DATA: AND (4) POSITIVE T-VALUES INDICATE GREATER MEAN VALUES FOR ISLE OF MAY.

(a) Early Season Females:	mean (s.e.) Isle of May (n = 202)	mean (s.e.) North Rona (n = 219)	d.f.	t-value	sig.
Width	47.8 (0.5)	49.5 (0.4)	419	−2.63	0.009
Length	146.5 (0.9)	139.4 (0.9)	419	5.79	<0.001
Estimated mass	152.4 (3.0)	152.3 (2.5)	419	−0.31	0.758
Mass:Length ratio	1.03 (0.02)	1.09 (0.01)	398.3	−2.78	0.006
(b) Late Season Females;	**mean (s.e.) Isle of May (n = 237)**	**mean (s.e.) North Rona (n = 371)**	**d.f.**	**t-value**	**sig.**
Width	44.1 (0.4)	47.7 (0.3)	534.9	−6.87	<0.001
Length	139.2 (0.7)	139.4 (0.7)	585.4	−0.16	0.874
Estimated mass	123.1 (2.1)	140.0 (2.1)	545.8	−5.32	<0.001
Mass:Length ratio	0.88 (0.01)	0.99 (0.01)	606	−6.53	<0.001
(c) Early Season Males:	**mean (s.e.) Isle of May (n = 19)**	**mean (s.e.) North Rona (n = 96)**	**d.f.**	**t-value**	**sig.**
Width	52.6 (1.1)	56.2 (0.7)	113	−2.32	0.022
Length	189.1 (1.8)	174.6 (1.4)	43.7	6.32	<0.001
Estimated mass	246.6 (8.5)	248.1 (5.7)	113	0.13	0.895
Mass:Length ratio	1.30 (0.04)	1.41 (0.02)	113	−2.06	0.042
(c) Late Season Males:	**mean (s.e.) Isle of May (n = 22)**	**mean (s.e.) North Rona (n = 93)**	**d.f.**	**t-value**	**sig.**
Width	49.6 (1.3)	53.1 (0.6)	113	−2.41	0.018
Length	174.9 (3.4)	174.9 (1.5)	113	0.02	0.986
Estimated mass	200.4 (10.0)	218.8 (4.9)	113	−1.74	0.084
Mass:Length ratio	1.14 (0.04)	1.24 (0.02)	113	−2.31	0.023

are made on sedated seals that are laid out to their maximum length, with the neck fully extended and nose to tail measurements taken from the tip of the tail which is held out parallel to the main axis of the body. Obviously, we cannot distinguish the tail (which is approximately 10 to 15 cm long) in our images, our measurements being from the nose to the end of the main body mass. Similarly, seals on the images are not sedated and are therefore observed in more natural postures. Despite these differences, the high resolution of the images used and the ability to control for elevation and flying height differences mean that our measurements from these images provide valuable indices of length and width. While it is not possible to combine these remote measurements directly with field measurements, our method provides the means to compare the relative morphology of large numbers of seals, both within and between sites. By contrast, our mass estimates from the remote measurements (136.6 kg $\pm$ 1.9 and 144.6 kg $\pm$ 1.7 for females at the Isle of May and North Rona, respectively; and 221.8 kg $\pm$ 7.5 and 233.7 kg $\pm$ 3.9 for males at the Isle of May and North Rona, respectively) are remarkably similar to mean seasonal values for males and females from the field data (139.9 kg $\pm$ 2.6 and 141.7 kg $\pm$ 1.3 for females at the Isle of May and North Rona, respectively, and 221.0 kg $\pm$ 2.8 for North Rona males), suggesting not only a useful index for comparison between images, but also a relatively accurate estimate of mass. Furthermore, the patterns of seasonal change observed in our remote measurements agree well with those observed from field measurements (Anderson and Fedak, 1985; Anderson and Fedak 1987b; Twiss, 1991). The regression models that we have used here to estimate mass from aerial photography are from a subset of the available data on grey seal morphology and mass relationships. However, we believe that they provide robust models, which require only two simple measures, length and width, for each seal on the aerial photographs and do not rely upon identifying individuals. In addition to these models, we also examined other model forms. Previous authors have utilized the equations of the form Mass $= 4.57 \times 10^{-5}$ (length $\times$ axilliary girth^2), or modifications thereof (Castellini and Kooyman, 1990; Castellini and Calkins, 1993). Using equations of this form with our field data provided R^2 values of 0.832 for females and 0.839 for males. However, these are based on axilliary girth rather than radius, and we could not directly determine girth from the aerial photography. Models for our field data, based on the form $\log(\text{mass}) = k + n\log(\text{axilliary radius}) + \text{length}$, provided R^2 values of 0.839 for females and 0.836 for males.

The advantages of the remote method described here are (1) a vastly increased sample size, (2) the ability to measure peripheral or otherwise inaccessible seals, (3) no disturbance to the seals, and (4) the ability to retrospectively assess seal sizes from aerial photographs. The limitations to this methods are (1) the lack of individual identity of study animals and (2) the reduced accuracy of measurement compared to hands-on field measurements. Clearly, direct field measurements are necessary for detailed studies of individual energy expenditure (Anderson and Fedak, 1985; Anderson and Fedak 1987a; Anderson and Fedak 1987b; Pomeroy *et al.*, 1999). However, in conjunction with these long term studies of individuals, the method presented here can be used to extrapolate such results to larger, colony-wide samples and examine intra-and inter-colony differences on a broad scale with relative ease.

Within-Site Seasonal Changes in Remotely Determined Seal Sizes

As expected from direct field measurements, females and males at both of our study colonies show seasonal reductions in mass as estimated from our remote measures of length and width. For the Isle of May, our data show that lengths of both males and females measured in the later part of the season are less than at the start of the season. This is consistent with a turnover of individuals, with later arrivals being shorter, lighter, and, therefore, younger individuals (Hewer, 1964; Anderson and Fedak, 1985; Anderson and Fedak, 1987b; Godsell, 1991; Pomeroy *et al.*, 1999). By contrast, neither males nor females at North Rona show significant differences in length between early and late season periods. As we know, there is a turnover of females at this site; therefore, these data suggest that later breeding females are of a similar length to earlier breeding females. As for the males, we are unable to say from these data whether these are the same males throughout or different individuals of similar length although Twiss (1991) and Twiss *et al.* (1994) demonstrate male turnover at the North Rona colony. Reductions in mass:length ratio at both colonies indicate that both males and females present in the latter half of the season are in relatively poorer condition than those present in the early part of the season.

Comparisons between North Rona and the Isle of May

Our data suggest that Isle of May females and males tend to be longer but thinner than their counterparts at North Rona. Consequently, both estimated mass and mass-to-length ratios are lower. As all variables tend to decline in magnitude through the season, the fact that there is an additional late-season survey for North Rona would tend to reduce the mean values at North Rona. Thus, differences for width, mass, and mass-to-length ratio may be conservative. Examining these inter-colony differences on a seasonal basis reveals that Isle of May males and females are only longer than their counterparts at North Rona during the early part of the season. Thus, the early season period at the Isle of May comprises the largest males and females. This has been shown to be true from field measurements of North Rona males (Anderson and Fedak, 1985) and females (Pomeroy *et al.*, 1999), though not as yet for the Isle of May.

Further Developments and Improvements of the Methodology

In the future, DEMs should be generated from true stereo-photographs, taken prior to the seal breeding season. This would provide "cleaner" DEMs without the errors induced by the use of non-stereo pairs, differing lighting conditions, sea level changes, and moving seals. Aerial photographs taken during the breeding season would then be ortho-rectified using this "clean" DEM, and seal lengths and widths would be digitized directly from these ortho-photographs. This would simplify the process and remove the need to account for potential errors generated through differences in camera elevation and angle. In addition, digitizing is the most labor intensive part of the methodology. We intend to examine methods of automating this procedure by use of image analysis, as adopted in Estep *et al.* (1994) who were able to classify seals from the background pack-ice. This approach is likely to prove more problematic for our images, because grey seals breed on substrates ranging from rocks to mud. Towards the close of the breeding season much of our study area forms a muddy quagmire, with seals being covered in mud. While we have opted for a simple but robust model for estimating mass, which relies on only two simple measures for each seal, more complex models, based on more measurements, can be used. Image analysis would also provide a rapid means of measuring seal sizes because the number of pixels (area) occupied by each seal can be used to estimate mass.

With over 12 years of aerial photography of UK grey seal breeding colonies (Hiby *et al.*, 1988), the method described here provides the means to conduct long-term retrospective studies of grey seal size and energetics. It also allows continued access to these data to complement targeted field studies of grey seal behavior and energetics. The methods we have employed could be readily adapted to any pinniped species for which similar data sources exist.

Acknowledgment

The work presented here forms part of a study funded by an NERC Fellowship to SDT. We thank Callan Duck, Dave Thompson, Lex Hiby, and Phil Lovell of the Sea Mammal Research Unit for access to the aerial photographs and all those who participated in fieldwork, in particular Larry Griffin, Phil Schwartz, and Roland Ascroft.

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(Received 22 September 1998; accepted 13 May 1999; revised 09 July 1999)