

# Abundance estimates of Southern Hemisphere Breeding Stock 'D' Humpback Whales from aerial and land-based surveys off Shark Bay, Western Australia, 2008

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## ABSTRACT

Single platform aerial line transect and land-based surveys of Southern Hemisphere Breeding Stock 'D' humpback whales *Megaptera novaeangliae* were undertaken off Shark Bay, Western Australia to provide absolute abundance estimates of animals migrating northward along the western Australian coast. The aerial survey flew a total of 28 flights, of which 26 were completed successfully, from 24<sup>th</sup> June-19<sup>th</sup> August 2008. The land-based survey was undertaken from Cape Inscription, Dirk Hartog Island, Shark Bay, during the expected peak of the whales' northward migration, from 8<sup>th</sup>-20<sup>th</sup> July. During the first week of the land-based survey, some double count effort was undertaken to provide information on the numbers of pods missed from the land station. The assumed period of northward migration was 2<sup>nd</sup> June-7<sup>th</sup> September. Estimated abundance of northward-migrating whales during that time is 33,850 (95% CI: (27,340-50,260)), representing an annual rate of increase of 12.7% (CV=0.19) since an estimate of 11,500 in 1999. This estimate is based on an estimate of relative abundance of surface-available whales of 11,100 (8,960-16,480), and an estimated  $g(0)$  of 0.33 ( $\pm 0.026$ ). There were considerable practical difficulties encountered during the land-based survey which reduced the effectiveness of the dual-survey approach for estimating  $g(0)$  for the aerial survey. Furthermore only about 15% of whales were estimated to be within the visual range of the land-based station. Alternative approaches for estimating  $g(0)$  from these data are therefore also presented, resulting in considerably higher estimates of around 0.6-0.7, and yielding a conservative abundance estimate of 17,500 (14,130-25,980).

## INTRODUCTION

Following increasing reports of humpback whale (*Megaptera novaeangliae*) sightings in winter off the western Australian coast in the early-mid 1970s, aerial surveys of humpback whales during their northward migration were undertaken from Carnarvon, Western Australia (WA) in an area off Shark Bay where aerial spotter and other data from whaling operations were available for the last year of humpback whaling, 1963. Results of those surveys to 1988 (Bannister *et al.*, 1991) demonstrated that significantly more whales were seen in the area in the 1980s than in 1963. Further surveys, in 1991 and 1994, demonstrated an annual increase rate of  $10.15 \pm 4.6\%$  to 1994 (see Bannister and Hedley 2001). In comparison to the estimated population size of 568 at the end of 1963 (Bannister, 1964), the population size in 1994 was calculated to be some 4000-5000 animals (Bannister, 1995).

The 1994 survey results showed that to detect a significant difference in population in future years, at an annual increase of 10%, an interval of three years would be required between surveys, leading to a proposed further survey in 1997. Given funding constraints, that survey took place in 1999, its aim being to provide an estimate of absolute abundance. This aim was more ambitious than for its predecessors, from which only a relative index had been obtained. The survey was planned to cover as much of the northern migration period as possible, with flights every other day over a two month period, mid June – mid August. Given the prevailing generally poor weather conditions, only 18 of the 30 planned flights could be flown, of which only 15 were completed. Nevertheless allowing for animals missed while submerged, 1999 population size was estimated as 8200-13600 (Bannister and Hedley, 2001).

Given the disappointing coverage, a further survey was planned to take place as soon as possible over the same period and area, but to include an additional land-based component. That survey took place in 2005; the results are reported in Paxton *et al.* (in press). Unfortunately, although the 2005 survey had been designed with the aim of improving on earlier surveys (which were only able to apply *ad hoc* corrections to adjust for uncertain trackline detection), last-minute logistical changes to the land-based survey in 2005 reduced its effectiveness. In particular, the location of the land-based survey had to be moved northward to a location where, in the event, whales often exhibited 'milling' behaviour rather than directional swimming more typical of migrating animals, and to where the offshore distribution of whales extended far beyond the visual range of the land-based observers.

Given rather equivocal results from the 2005 survey, improvements to the design of the 2008 survey were planned as follows:

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- 50 1. The aerial survey component was expanded in area to extend offshore coverage (following some  
51 experimental work in 2007 to determine the most appropriate survey area).
- 52 2. Aerial survey data were collected using a direct data acquisition system.
- 53 3. The land-based component of the survey was expanded to include some double-platform  
54 independent observer counts, and thus allow estimation of a correction factor for whales missed by  
55 the land-based observers.
- 56 4. The location of the land-based platforms was at Cape Inscription, Dirk Hartog Island, Shark Bay.  
57 From previous surveys, it was expected that whales passing this location would be more  
58 identifiable as ‘northward-migrating’ and furthermore, that they would pass closer to the shore at  
59 this latitude.

60 This report details the analysis of data from the 2008 survey, the aerial component of which took place from 24  
61 June-19 August, with the land-based component from 8-20 July.

## 62 FIELD METHODS AND DATA

### 63 Aerial survey

64 In 1999, most sightings were made within about 30km of the eastern edge of the survey area – an area of  
65 coastline delineated by the western coastlines of Bernier, Dorre and Dirk Hartog Islands (see Bannister and  
66 Hedley, 2001), although the transects had extended out to about 56km from those islands. In 2005, the sightings  
67 were spread more evenly (in relation to distance offshore) throughout the survey area (Paxton *et al.*, in press). A  
68 small set of flights in 2007 over the same area but with two legs extending 92km offshore (to 112°E) suggested  
69 that humpback whales might be found out to 65km offshore (i.e. to about 112° 25’E) but with only a very few  
70 further out. The 2008 flight path was therefore planned to cover an area reduced in latitudinal coverage from that  
71 surveyed previously, approximately 55km x 75km immediately west of Dorre and Dirk Hartog Islands on the  
72 western boundary of Shark Bay. The reduction in latitudinal effort allowed for two extended transect legs of  
73 about 70km length to be flown to provide information on the possible distribution of animals further offshore.  
74 These were located off the north of Dirk Hartog Island. In addition, on seven flights when the land-based survey  
75 was operating, short legs of about 20km were flown at the latitude of Cape Inscription. The survey area and a  
76 typical flight path are shown in Figure 1. The approximate length of the two most northerly and two most  
77 southerly east-west transects was 45-50km. The survey area covered a region of approximately 6570km<sup>2</sup>.

78

79 *[Figure 1 about here]*

80

81 As in 1999 and 2005, the 2008 survey flights were undertaken from a high-wing, twin-engine aircraft, mainly a  
82 Partenavia P68B (fitted with bubble windows), under charter from TropicAir Services Pty Ltd, flying out of  
83 Carnarvon, WA. On four flights, a Cessna 337 (with flat windows) was chartered from Norwest Air Work Pty  
84 Ltd, based in Exmouth, WA. On all flights, a GPS and on-board computer system were available to plot  
85 waypoints (as on previous surveys) and to log data (such as time, position and altitude); in addition, in 2008  
86 *Cyclopes* software (Kniest, unpublished) was employed to map the flight path. Separately for each side of the  
87 aircraft, the two observers recorded various weather covariates, including *glare strength* (a factor with four  
88 levels); *glare angle*; *Beaufort sea state*; *wind strength* (in knots); *wind direction*; *percentage cloud cover*; and  
89 ‘*sightability*’, a subjective overall assessment of the sighting conditions (a factor with four levels). Observers  
90 used a clinometer (industry standard Suunto PM-5/360PC) and an angleboard to measure declination and  
91 horizontal angles to sightings. For each sighting, observers made every effort to record pod size and swimming  
92 direction. All sighting details were recorded on a Sony digital recorder for post-flight data entry. A total of four  
93 observers participated in the survey, with their levels of participation ranging from flying 24 of the 28 flights  
94 (85%) down to 7 (25%).

95 Of the 28 flights flown, 26 of were successfully completed and included in the analysis. The first three flights  
96 (on 24, 26 and 29 June) were flown in a northerly direction; the remainder were flown in a southerly direction.  
97 Because of glare, usually the latter is preferable for surveys in this location; historically (when transects were  
98 closer together) such a strategy has also been used in order to minimise the risk of double-counting animals  
99 (flying was in the opposite direction to the whales’ migration path).

100 Table 1 details the date, total transect length and number of sightings for each flight. ‘NM’ sightings are those  
101 pods recorded with a northward swimming (migration) direction. NM+ sightings additionally include some pods

102 of undetermined direction, randomly allocated to be travelling north in proportion to the sightings of known  
 103 direction on a given day which were travelling northwards.

104

105 [Table 1 about here]

106

107 **Land-based survey**

108 *Sighting survey*

109 The land-based survey took place from Cape Inscription, on the northern end of Dirk Hartog Island – a rugged  
 110 and exposed area with virtually no facilities at the site. The observation site was low, with the highest accessible  
 111 point being just 25.5m above sea level

112 Survey effort was scheduled for 9 hours each day from 8-20 July; 7 full days were completed together with three  
 113 partial days (of 6, 7 and 2.5 hours respectively), with no effort possible on 11 and 20 July. During the first survey  
 114 week (8-13 July), 5 hours of double-platform (independent observer) data were also collected on each day with  
 115 suitable survey conditions (25 hours in total), with four observers assigned to each of the two teams ('Car' and  
 116 'Bush'). During the second week, reduced personnel resulted in it only being feasible to conduct single-platform  
 117 survey; these observations were augmented by 'focal follows' (i.e. each surfacing of a detected pod recorded  
 118 until out of visible range) without disruption to the sightings survey.

119 Whales were spotted by the observers and sightings were input directly into a notebook computer running  
 120 *Cyclopes* (Kniest, unpublished) – software specifically designed for the tracking of marine mammals. A  
 121 theodolite, connected directly to the notebook computer, was also used to measure the positions of passing  
 122 groups of whales in *Cyclopes*. One observer operated the theodolite, while another operated the computer. When  
 123 a sighting was made, the theodolite operator pointed the theodolite at the surfacing pod and with the push of a  
 124 button, vertical and horizontal bearings were transmitted to, and recorded directly in, *Cyclopes*. The position of  
 125 the pod was calculated correcting for tides, curvature of the Earth and refraction, and was plotted on a map of the  
 126 area. The computer operator added data on pod composition, behaviour and direction of travel, when these could  
 127 be determined. *Cyclopes* was thus able to compute pod speed, course and distance from any reference point. For  
 128 each pod sighted the following information was also recorded using *Cyclopes*: time (to the nearest second);  
 129 unique pod identifier (A, B, C, etc.); species confirmation; calf presence; and cue, plus other relevant  
 130 information such as whether or not the group went into or came from the Shark Bay area to the east of the  
 131 islands (see Figure 1). Whilst perpendicular distance offshore was rarely observed, it was calculable for pods  
 132 with at least one fix either side of the 'abeam' line from the land-based platform.

133 The other two observers were 'spotters' who used naked eye or 7x50 binoculars to sight whales. The spotters  
 134 were allocated adjacent sectors of the ocean to scan to spread sighting effort as much as possible. Each land-  
 135 based team attempted to record the behaviour and all surfacings of every sighted group to increase chances of  
 136 matching between the two land-based teams and the aerial survey. Inevitably however, this was not possible  
 137 during periods of high densities of whales. Pods further offshore had an increased risk of being 'lost', only  
 138 sighted once, or being confused with other pods at a similar bearing. Spotter observations were entered as  
 139 'additional observations'. The information above was entered for each 'additional observation' and the position  
 140 was calculated from the bearing and reticule readings taken from the binoculars. Priority for theodolite fixes was  
 141 given to new pods, after which, theodolite effort was spread as evenly as possible among the pods being tracked  
 142 in the study site. Pods only sighted once or a small number of times in which group composition could not be  
 143 accurately determined were counted as 1 animal (unless more than one animal had been spotted). For the double-  
 144 platform data, an assessment of duplicate status was also recorded.

145 Weather conditions were recorded hourly and at the beginning and end of each day. Data recorded included sea  
 146 state, swell height and direction, wind speed and direction, cloud cover (in oktas), glare (degrees of view  
 147 obscured by glare) and other factors affecting visibility (e.g. smoke, haze, squalls).

148 Post data collection, all *Cyclopes* files were reviewed by the (primarily volunteer) researchers each evening and  
 149 then, for consistency, by an experienced researcher (RAD), who has carried out the same type of work on  
 150 previous land-based humpback whale surveys off the east coast of Australia.

151 In the event, a large proportion of the whales migrated past Cape Inscription at considerable distances from the  
 152 shore, resulting not only in a high proportion of whales being missed, but also in difficulties obtaining theodolite  
 153 fixes required for tracking of pods and accurate distance estimation. Beyond about 8km, whales were sighted 'on

154 the horizon'; thus recorded distances > 8km could not be considered reliable. The researchers recommended  
 155 exclusion of all sightings beyond 12km as there was no accuracy in these measurements.

156 The matching process (undertaken by RAD) was severely hampered by the distance inaccuracies, but is assumed  
 157 to have been completed without error in this analysis (i.e. no account is taken of incorrect duplicate  
 158 identification). A summary of the land-based survey data is shown in Table 2. The number of NM and NM+  
 159 pods sighted is given, together with two further datasets: (1) the number of sightings after truncation at 12km  
 160 offshore (and excluding pods for which no offshore distance was available; and (2) the number of sightings after  
 161 truncation at 12km offshore (and including those pods with no offshore distance).

162

163 *[Table 2 about here]*

164 *Focal follows*

165 In addition to the survey data, a total of 22 focal follows were conducted during the land-based survey, primarily  
 166 during the second week of the survey. During single platform survey, the focal follow team tracked randomly-  
 167 selected pods of a range of sizes and composition (singletons, mother and calf groups and multiple adult groups)  
 168 using a theodolite linked to *Cyclopes*; an additional observer (with binoculars) aided in keeping track of the  
 169 group. The minimum time for a focal follow was 20 minutes (which encompassed at least three surface intervals  
 170 and three deep dives). Surface intervals included shallow dives ('breathing dives') in which the animals  
 171 disappear for a matter of seconds (usually no longer than 1 minute) before returning to the surface to breathe.  
 172 These were differentiated from 'deep dives' in which the animals disappear for a number of minutes. For each  
 173 surfacing of the followed pod, the length of surface interval, mean travel speed during the surface interval and  
 174 number of blows/breaches and surface-active behaviours (all surface behaviours such as breaches, pectoral slaps,  
 175 tail slaps and unidentified surface behaviours) per whale per minute of surface time were estimated. For each  
 176 deep dive, the dive time and mean travel speed during the dive were also estimated. From these data, the mean  
 177 dive time, surface interval, blow rate, breach rate, surface-active rate and speed of travel were calculated for each  
 178 pod followed. Focally followed pods were limited to those considered to be travelling north.

## 179 ANALYSIS METHODS

### 180 Overview

181 The survey objective was to estimate the absolute abundance of northward-migrating humpback whales off  
 182 Shark Bay. The aim of the aerial survey component was to estimate the number of whale pods seen on a given  
 183 flight. This number would then require a correction so that it corresponded to the number of pods passing  
 184 through the area during a given time, say, per day. Such a correction factor would depend on the whales' speed  
 185 of travel during their northward migration. Without further adjustment, the number of pods per day would be an  
 186 underestimate of the true number, since uncorrected estimates only estimate the number of whales at the surface  
 187 and thus available to be seen. In addition to this 'availability' bias, not all whales at the surface are detected,  
 188 leading to so-called 'perception' bias (Marsh and Sinclair, 1989).

189 The aim of the land-based survey component was threefold: (1) to provide an estimate of absolute abundance of  
 190 northward-migrating humpback whale pods during the two weeks of the aerial survey (and thus allow calibration  
 191 of the corresponding aerial estimates); (2) using the focal follow data, to provide estimates of whale migration  
 192 speed; and (3) to provide estimates of mean pod sizes (since it was expected that these would be underestimated  
 193 from the aerial survey).

194 Combining the results from the two components, estimates of the absolute number of northward-migrating  
 195 whales passing through the survey area for each day of the aerial survey may be obtained. Fitting a model to  
 196 these estimates (to allow prediction of the number of whales passing through the area on non-survey days,  
 197 including those at the very beginning and end of the expected period of northward migration), and integrating the  
 198 fit throughout the migration period, yields an estimate of absolute abundance of northward migrating whales.

### 199 Modelling the aerial survey data to obtain relative density estimates

200 Note that in what immediately follows, 'density' refers to 'relative density', since no account for perception nor  
 201 availability bias has been made (i.e. in this section,  $g(0)$  is assumed to be equal to one).

202 For each flight, pod density is estimated using a spatial generalized additive model (GAM) similar to the 'count  
 203 model' of Hedley and Buckland (2004). The response variable of the model is the number of pod sightings per  
 204 'segment' of the transect, where the segment length must be specified but should be selected such that sighting

205 conditions (and geographic location) do not change appreciably within a segment. An offset variable is included  
 206 in the model to account for differences in estimated probabilities of detection within each segment, and  
 207 consequential potentially different effective search areas of the segments. The offset is estimated using multiple  
 208 covariate distance sampling – single platform line transect estimation but with the ability to include covariates  
 209 (such as sea state) in the scale parameter of the detection function (Marques and Buckland, 2003).

210 With a logarithmic link function, the general form of a GAM of this type may be written

$$211 \quad E[n_i] = \exp \left\{ \log(2l_i w \cdot \hat{p}_i) + \sum_k f_k(z_{ik}) \right\},$$

212 where  $E[n_i]$  is the expected number of sighted pods in the  $i^{\text{th}}$  segment and  $\text{Var}[n_i]$  is assumed to be proportional  
 213 to this;  $l_i$  is the length of segment  $i$ ;  $w$  is the perpendicular (right-) truncation distance;  $\hat{p}_i$  is the estimated  
 214 probability of detection of a pod in segment  $i$ ;  $z_{ij}$ ,  $j=1, \dots, k$  denotes the value of the  $j^{\text{th}}$  (spatial) covariate in the  $i^{\text{th}}$   
 215 segment; and the  $f_k$  are (smooth) functions. Extending this form, it is feasible for a function  $f_j$  to depend on more  
 216 than one covariate (e.g.  $f(\text{lat}_i, \text{lon}_i)$ ), and/or for the covariate to be temporal (e.g. *day*).

217 Hedley and Buckland (2004) suggested that variance from a spatial model of this type may be estimated using an  
 218 appropriate resampling scheme such as a non-parametric or parametric bootstrap. In practice, these bootstrapping  
 219 techniques frequently give biased results when smoothing models. Wood (2006, p246-7) proposed an alternative  
 220 approach which can be much simpler to implement, and appears not to suffer from the bias often associated with  
 221 the bootstrapping approaches. This approach uses a ‘prediction matrix’ to map the model parameters to the  
 222 predictions of the linear predictor, in conjunction with simulation from the posterior distribution of the  
 223 parameters. The analysis in this report uses Wood’s (2006) approach, conditioning on the estimated smoothing  
 224 parameters.

225 The offset in the model above includes an estimate,  $\hat{p}_i$ , of the probability of detection. Whilst a bootstrapping  
 226 approach could be implemented to include variance in this estimate, as noted above bootstrapping spatial models  
 227 often gives unstable and biased results. An alternative method of propagating the uncertainty in this estimate has  
 228 been implemented in this analysis. The idea is currently being developed (Bravington *et al.*, in prep.). A matrix  
 229 of first derivatives of  $\log(\text{eff.area}_i) = \log(2l_i w \cdot \hat{p}_i)$  with respect to the parameters of the detection function is  
 230 included in the linear predictor. The Hessian matrix from the likelihood maximization of the detection function  
 231 describes the local curvature of the fit associated with the parameter estimates; its value(s) are used in the model  
 232 fitting process also (as a prior on the variance of a parameter to be estimated by the spatial model). Algebraic  
 233 details are given in the Appendix.

### 234 **Estimating mean pod size**

235 Results from other studies have shown that aerial survey pod size estimates can be negatively biased, since the  
 236 animals are in view only for a relatively short period of time. In contrast, some pods sighted from the land station  
 237 could be tracked for over an hour, although such pods would tend to be those migrating closer inshore so may  
 238 not necessarily be representative of all migrating pods.

239 In order to estimate mean pod size, we compared three methods: (a) the mean size of pods sighted from the  
 240 land-based station within 12km; (b) the mean size of pods sighted within 0.7km of the trackline from the aerial  
 241 survey; and (c) truncating at 0.7km as for method (b), a spatial model for estimated pod size was fitted to  
 242 examine variation in pod size within the survey region. For method (a), 12km was selected as a truncation point  
 243 beyond which recorded pod sizes were considered less reliable. For methods (b) and (c), 0.7km was selected as a  
 244 truncation distance within which pod size did not affect detectability (i.e. to eliminate potential ‘size bias’  
 245 effects).

### 246 **Estimating abundance from the land-based survey data**

247 Within the visible range of the land-based observers (here, up to 12km offshore), the number of northward-  
 248 migrating whales passing the land station per watch period (where a ‘watch’ is defined as a 3 hour period within  
 249 a day, say) gives an estimate of their rate of passage. Using the double-platform data from the first survey week,  
 250 logistic regression (Buckland *et al.*, 1993; 2001, p. 360-3) may be used to estimate the proportion of whale pods  
 251 missed. Three correction factors for pods missed are estimated, depending on the mode of survey operation at the  
 252 time (i.e. ‘Car’ Platform only, ‘Bush’ Platform only, or Double Platform). It is assumed that the probability of  
 253 detection of a pod from one platform is independent of whether it is detected from the other, and independent of  
 254 whether other pods are detected by either platform. Detection probability may be modelled as a function of  
 255 covariates. The counts from each watch are then adjusted according to the mode of survey operation. Summing,

256 and standardizing for different hours of effort, daily estimates of pod abundance may be calculated. The  
 257 estimates correspond to the survey region in view from the land-based station only.

## 258 RESULTS

### 259 Use of the aerial data

260 Prior to analysis, transect line lengths were calculated from the GPS positional data using R code adapted from  
 261 Visual Basic *Geofunc* functions (J.L. Laake, unpublished). Corresponding formulae are given in Zwillinger  
 262 (2002). Heading angles were corrected for aircraft drift angle, and perpendicular distances ( $x$ ) to sightings were  
 263 calculated using the following simple tangent formula (e.g. Pike *et al.*, 2008):

$$264 \quad x = h(\tan(90 - \theta))\sin(\phi),$$

265 where  $h$  is altitude;  $\theta$  is declination angle to the sighting; and  $\phi$  is drift-correcting heading angle.

266 During the aerial survey, the swimming direction of sighted pods was recorded where possible. Since the  
 267 objective of the survey is to obtain estimates for the northward-migrating component of the population only, then  
 268 the swimming direction is critical. Out of 855 pods with either a swimming direction recorded, or designated as  
 269 'milling', then 571 (67%) of these were recorded as travelling northwards (where NE and NW were classified as  
 270 North). In total, 1357 humpback (including 'possible' humpback) pods were recorded whilst on effort and 42%  
 271 of these were recorded as travelling northwards. As in Paxton *et al.* (in press), humpbacks with no direction  
 272 recorded (and not milling), were randomly allocated a swimming direction according to the relative proportions  
 273 of directions observed on a given flight. This increased the sample size considerably to 920 northward-migrating  
 274 whales (seen on effort). Hereafter, we analyse the data for whales recorded as travelling north (NM whales)  
 275 separately from a dataset of NM whales augmented by sightings with unknown swimming direction, but  
 276 randomly allocated to be travelling northwards (NM+ whales).

### 277 Detection function estimation: aerial data

278 Two aircraft were used on the aerial survey: the Partenavia, fitted with bubble windows, and the Cessna, with  
 279 flat windows. Angles of declination taken from each aircraft suggested that strips of about 80m (40m either side  
 280 of the trackline) and of about 260m were obscured from the view of observers immediately beneath the  
 281 Partenavia and the Cessna respectively. Histograms of perpendicular distances suggested that some pods were  
 282 being missed beyond this strip for the Partenavia, perhaps because it was uncomfortable for the observers to look  
 283 down at such an angle. The problem was alleviated by extending the left-truncation distance to 260m for both  
 284 aircraft; thus about 6% of the sightings were excluded from further analysis (see Table 1).

285 Initial exploratory analyses of the NM aerial line transect data were conducted in *Distance* v5.0 (Thomas *et al.*,  
 286 2010), and model selection for both NM and NM+ whales was based on these analyses. Potential factors or  
 287 covariates included *Cloud cover*, *Sightability*, *Side of Aircraft* (Port/Starboard), *Sea state*, *Wind speed*, *Observer*,  
 288 *Pod size* and *Aircraft*. The detection function was modelled as a function of perpendicular distance, and these  
 289 variables were considered for inclusion via the scale parameter of this function (either a hazard-rate or a half-  
 290 normal form). The perpendicular distance data were right-truncated at 3.0km for NM whales and 4.5km for NM+  
 291 whales. A stepwise forward selection procedure (starting with a model containing perpendicular distance only)  
 292 based on Bayes' Information Criterion (BIC) was used for model selection.

293 For both NM and NM+ pods, the model selected by BIC alone would have included *Pod size*. However the fitted  
 294 detection function from such a model was such that estimated probability of detection decreased as pod size  
 295 increased, counter to expectation. For NM+ pods, the BIC also suggested a model including *Sightability* was  
 296 better than a perpendicular-distance-only model. Similarly to pod size, however, probability of detection was  
 297 estimated to be lower in 'Excellent' conditions than in 'Good' and 'Poor' conditions. The other covariates were  
 298 not found to significantly improve upon a perpendicular-distance-only fit, and so in the absence of an  
 299 explanation for the relationship between detectability and *Pod size*, or between detectability and *Sightability*,  
 300 half-normal models of perpendicular distance only were fitted to both the NM and the NM+ data. Fitted  
 301 detection functions are shown in Figure 2. Estimated effective strip half-widths were 2.05km ( $\pm$  0.088) and  
 302 2.46km ( $\pm$  0.084) respectively.

303

304 [Figure 2 about here]

305 **Mean pod size estimation**

306 Pods seen from the land-based survey ranged in size from 1-6 whales, with most groups sighted as singletons or  
 307 pairs. During the Double Platform component of this survey, only about half of the pod sizes recorded was in  
 308 agreement between the two platforms. Estimated mean pod size from the land-based survey varied from about  
 309 1.7 ( $\pm 0.084$ ) to 1.85 ( $\pm 0.056$ ), depending on the subset of data selected.

310 As for the land survey, most pods sighted from the air were of 1 or 2 whales; pod size ranged from 1-8. No  
 311 spatial or temporal trend in pod size was detected from the aerial data, and there was no evidence of 'size bias'.  
 312 In fact, as noted above, any effect of pod size on detectability appeared to be in the 'wrong' direction. Mean pod  
 313 size from the aerial data was estimated as 1.80 ( $\pm 0.043$ ) for NM whales. The point estimate for NM+ whales was  
 314 considerably lower at 1.64 ( $\pm 0.032$ ), but this is perhaps not surprising, since this data set includes pods for which  
 315 a swimming direction was not recorded, and presumably pod size would also be more difficult to ascertain for  
 316 such pods also (and would tend to be under-estimated). Note therefore, that in this analysis for both NM and  
 317 NM+ estimates, the mean pod size of 1.80 was considered most appropriate and used for all conversions from  
 318 pod density to whale density.

319 **Land-based survey**320 *Sighting survey*

321 Since sightings from the aerial survey extended far beyond the visible range of the land station, it was clear that  
 322 an 'abundance' estimate from the land-based survey, even for the two weeks of its duration, would only  
 323 represent a proportion of the migrating population. In this section, the estimate calculated corresponds to  
 324 migrating animals passing within 12km of the shore. To use this estimate for calibration of the aerial estimates  
 325 below requires abundance to be estimated for a corresponding region from the aerial survey (see 'Calibration of  
 326 aerial survey').

327 To estimate the number of pods missed within 12km offshore during the land-survey, the double count data  
 328 collected during the first week of that survey were fitted using logistic regression (Buckland *et al.*, 1993; 2001).  
 329 In order to obtain a reasonable sample size, the model was fitted to NM+ data. Potential covariates were *team*,  
 330 *distance offshore*, *sea state*, *glare width*, *wind speed*, and *pod size*, and interactions of the latter variables with  
 331 *team*. The final model was selected by AIC using a backwards stepwise algorithm. The number of pods seen by  
 332 at least one land platform was 74; this was reduced to 49 after truncation at 12km. Covariates selected for the  
 333 untruncated data were *team* and the interaction term *team:distance offshore*. When the data were truncated at  
 334 12km offshore, an additional interaction term *team:pod size* was also selected. The number of pods seen on each  
 335 watch period of the land survey was then adjusted according to the estimated correction factors (depending on  
 336 which platform was operating) in Table 3. Since there was some daily variation in the number of hours of survey  
 337 effort, the estimates were also standardized by effort. Using a mean pod size estimate of 1.80, estimates for NM  
 338 whales corrected and standardized to 9 hours per day are shown in Figure 3. Data from 18<sup>th</sup> July, on which day  
 339 there were 2.5 hours of effort, were excluded from the analysis. The total estimated number of pods was 154  
 340 (totalling 276 whales).

341 *[Figure 3 about here]*

342

343 *[Table 3 about here]*

344 *Focal follows*

345 A total of 17 focal follows was carried out in week 2 (this small sample size was due to the amount of down time  
 346 due to poor weather conditions). An additional 5 pods were focally followed in week 1, when the emphasis for  
 347 two team effort was on obtaining double-platform count data. Pod compositions were 3 singletons, 11 pairs, 3  
 348 mother and calf groups, and one of each of a group of 3, 4, and 5 adults. The data are summarized in Table 4. As  
 349 there was only a total of 22 focally followed pods, speed of travel, surfacing time and dive time were calculated  
 350 averaging across all pod compositions. This assumption seemed quite reasonable for speed and dive time  
 351 calculations; more variation across pod composition was evident in time spent at the surface (which includes  
 352 time spent 'shallow diving', but for which it is considered that whales would still be visible from the air). The  
 353 average speed of travel was calculated as 5.56km/h ( $\pm 0.31$ ); the mean proportion of time spent underwater was  
 354 0.43 and at the surface 0.57.

355

356 *[Table 4 about here]*

357

358 **Spatio-temporal model of the aerial data**

359 Transects covered on effort were divided into segments of length approximately equal to 10 nmiles (18.5km),  
 360 and the number of pods sighted in each segment was calculated. For each segment, an offset variable was  
 361 computed as the logarithm of the effective area of the segment, where the effective area is given by twice the  
 362 segment length multiplied by the estimated effective strip half-width from the detection function estimation  
 363 described above. Potential spatial covariates were *Latitude*, *Longitude* and *Bottom depth* – sourced from a 1' by  
 364 1' grid from the U.S. National Geophysical Data Center, NOAA Satellite and Information Service  
 365 ([www.ngdc.noaa.gov/mgg/bathymetry](http://www.ngdc.noaa.gov/mgg/bathymetry)). In addition, *Day* or alternatively, *Week* (where Day 1 – and the first day  
 366 of Week 1 – was defined to correspond to 2 June, the assumed start of the whales' northward migration period)  
 367 were potential temporal covariates.

368 Model fitting and model selection were conducted in the *mgcv* package (Wood, 2008) available in R (R  
 369 Development Core Team, 2008), with inflated model degrees of freedom to reduce the tendency of generalized  
 370 cross validation to overfit (Kim and Gu, 2004). A number of forms for the smoothing components of the spatial  
 371 models were considered, but none of these showed evidence for including *Bottom depth* in the model. GCV  
 372 score was used to compare models; the final selected model was a tensor product smooth (Wood, 2006) of a two-  
 373 dimensional thin-plate spline of *Latitude* and *Longitude*, and a thin-plate spline of 'Day'.

$$374 \quad \log [E(nsight_i)] = te(Latitude_i, Longitude_i, Day_i) + \log(estimated\ effective\ area_i) + X_i$$

375 where  $Var(nsight_i)$  was assumed to be proportional to  $E(nsight_i)$ , and  $te$  is a tensor product of thin-plate spline  
 376 smooths of *Latitude* and *Longitude*, and *Day*. The offset variable for the  $i^{th}$  observation,  $\log(estimated\ effective$   
 377  $area_i)$ , was estimated using the effective strip widths estimated from the distance sampling analysis.  $X$  is a vector  
 378 of first derivatives and was used to propagate variance, penalized according to the Hessian of the respective  
 379 detection function fit. Estimation of tail densities (before the first flight of the season and after the last) was  
 380 improved by adding two zero counts to the data, one on 2<sup>nd</sup> June and one on 7<sup>th</sup> September.

381 Integrating across the predicted density surfaces for each day within the assumed migration period gave snapshot  
 382 estimates of abundance. To convert these estimates into daily estimates, the rate of passage through the survey  
 383 area was estimated using an average speed of travel of travel of  $5.56\text{kmh}^{-1}$ . The latitudinal width of the survey  
 384 area was 86.7km, hence the snapshot estimates were multiplied by a correction factor equal to  $(5.56 \times 24)/86.7$  to  
 385 convert them to daily estimates. (Estimated variance in speed of travel was not incorporated in the variance of  
 386 the final abundance estimates.) Multiplying by the estimated mean pod size resulted in daily estimates of whale  
 387 abundance, uncorrected for availability and detection bias (Figure 4). Total relative abundance was 11,100  
 388 (8,950-16,430) for NM whales and 13,660 (11,310-18,800) for NM+ whales (Table 5).

389 For illustrative purposes, a similar model with *Week* instead of *Day* was also fitted, yielding the plots shown in  
 390 Figure 5. These demonstrate how the distribution of whale pods varied during the course of the migration period.  
 391 At the latitude of Cape Inscription, the estimated pod density as a function of distance offshore (averaged over  
 392 flights during the two weeks of the land-based survey – i.e. weeks 7 and 8) is shown in Figure 6. These plots  
 393 indicate that density in week 7 increased gradually with distance offshore to a peak at around 30-35km offshore.  
 394 During week 8, peak density was over a larger distance, at around 20-35km offshore. In both weeks, estimated  
 395 density was very low beyond about 60km offshore. Within the region of the land-based station (lower panels of  
 396 Figure 6), the increase in density with distance offshore was slightly greater (and slightly more pronounced)  
 397 during the second week.

398 *[Figures 4, 5 and 6 about here]*

399

400 *[Table 5 about here]*

401 **Calibration of the aerial survey**

402 From the land-based survey, we have two sets of estimates of pod abundance:  $\hat{N}_{9L_1}, \hat{N}_{9L_2}, \dots, \hat{N}_{9L_{10}}$  for NM and  
 403 for NM+ pods. (The subscript '9' denotes for the 9 hour period of a standard survey day;  $L$  denotes 'land-based  
 404 survey' and these are for the 10 days for which there was at least 6 hours of survey effort.) Notwithstanding the  
 405 difficulties in recording data from the land owing to the distances offshore at which many of the whales  
 406 migrated, these estimates only correspond to the visible land-based survey region (here, assumed to be about  
 407 12km offshore).



408 From the aerial survey, we again have two sets of estimates of pod abundance, one set for NM pods and one for  
 409 NM+ pods. These snapshot estimates are available not only for the days on which flights were flown, but by  
 410 predicting from the spatio-temporal model above, also for any day within the assumed migration period. In order  
 411 to use the land-based estimates for calibration of the aerial estimates, the calibration must correspond to the same  
 412 survey region and over the same time period.

413 Since only about 15% of pods passed within the visible land-based survey region, the calibration approach  
 414 adopted here is as follows:

- 415 (1) estimate ‘snapshot’ abundance for the seven 1’ by 1’ gridsquares at the latitude of Cape Inscription, for  
 416 the corresponding ten days of the land-based survey;
- 417 (2) convert these to 9 hour estimates (using the estimate of speed of travel of 5.56km/h and a latitudinal  
 418 width of 1.856km)
- 419 (3) fit a linear regression model (with no intercept) to estimate the slope of the regression of aerial  
 420 estimates against land estimates; the slope is the calibration factor.

421 As would be expected, the calibration factor estimate varied substantially according to which subset of data was  
 422 used for the calibration. We considered NM and NM+ pods separately, but took no account of possible  
 423 differences in recording direction of travel between the two surveys. Because of the large number of land-based  
 424 sightings that had no offshore distance recorded, a set of results was generated which included land-based  
 425 sightings with offshore distances within 12km *plus* sightings with a missing offshore distance. This set of results  
 426 gave an indication of the sensitivity of the results to the dataset used. The estimated total number of pods from  
 427 the land-based survey increased by about 70-75%; the calibration factor went down by about 40-50%. The  
 428 estimated calibration factors ( $\hat{g}(0)$ s) are shown in Table 5; applying these factors gives total whale abundance  
 429 ranging from 17,500 (95% CI: 14,130-25,980) to 36,600 (95% CI: 30,310-50,190).

## 430 DISCUSSION

431 The estimates presented in Table 5 are very different, significantly so for the two rows of data which represent  
 432 different subsets of the land-based data. The land survey was not particularly successful in providing a suitable  
 433 ‘calibration’ for the aerial survey estimates, i.e. one that accounted for bias due to a lack of availability of diving  
 434 pods and due to pods at the surface being missed. This is primarily due to the high proportion of animals that  
 435 were beyond the range of the land-based observers, and so the overlap between the aerial survey – already for  
 436 only a few days – was also spatially limited. Additionally, there may be some issues related to the different  
 437 relative abilities of the aerial and land-based survey to identify the direction of a sighted pod. During the land-  
 438 based survey, for pods sighted sufficiently closely for tracking purposes, recording direction was straightforward  
 439 whereas for the aerial survey, determination of swimming direction was generally based on fewer cues over  
 440 much shorter periods of time in view.

441 The primary objective of the 2008 survey was to obtain an estimate of absolute abundance of northward-  
 442 migrating whales. Whilst we can be reasonably confident about the relative estimates presented in Table 5, there  
 443 is wide variation in the absolute estimates as a result of substantially different estimates of  $g(0)$ . *A priori*, from  
 444 previous analyses and studies elsewhere, estimates in the range 0.3-0.4 or so might have been expected, with  
 445 such an estimate correcting for both availability and perception biases. It is therefore necessary to investigate  
 446 further the reasons for the evidently much higher  $\hat{g}(0)$ s reported here. The estimation method used by Paxton *et*  
 447 *al.* (2005) estimated an ‘availability curve’ indicating the true (relative) density of pods with distance from shore.  
 448 Within the region of the land-based observers, this showed a steady increase in density with distance offshore, up  
 449 to a peak at around 10km. The detection function fitted to the distances offshore (using the land-based data)  
 450 showed a very steady decrease in detectability with distance, based on a half-normal detection function.  
 451 Differences between the two curves were used to correct the counts from the land-survey for pods missed from  
 452 the land, and then  $g(0)$  was estimated by comparing the aerial abundance in the region with the land-based  
 453 abundance, over the two-week period of the land-survey in 2005. The correction factor applied to the land data  
 454 for each day was about 1.5 (C.G.M. Paxton, pers. comm.) The data for the 2008 survey were markedly different  
 455 from those obtained in 2005. Furthermore, they were very different even between the two weeks of the land  
 456 survey duration (Figure 7). The improvement to the design of the 2008 survey meant that the estimated number  
 457 of pods missed from the land was able to be estimated from the double-platform effort during the first week of  
 458 that survey, yielding correction factors by platform operation (see Table 3). The number of pods on which these  
 459 calculations were based was 73 if the data were not truncated; it decreased to only 48 if the data were truncated  
 460 at 12km. The estimates of Table 3 appear reasonably plausible compared with other studies of migrating  
 461 populations, but if anything perhaps a little lower than might be expected, especially given the distances offshore  
 462 at which the whales passed. If the estimates of Table 3 are in fact negatively biased, then the estimates of  $g(0)$

463 would be lower (and abundance consequentially higher). Aside from the problems of the offshore distribution of  
 464 the whales in 2008, the double-platform land-based approach to estimate the number of pods offshore would be  
 465 preferable to the aerial-land calibration, since the data would be expected to be more reliable.

466

467 [Figure 7 about here]

468

469

470 An alternative approach based directly on surface availability of pods (Barlow *et al.*, 1988) to estimate a  $g(0)$   
 471 correction for availability bias was implemented in Bannister and Hedley (1999) in their analysis of the 1999  
 472 survey data:

473

$$P(\text{being visible}) = (s+t)/(s+d)$$

474 where  $s$  is the average time a whale stays at the surface;  $d$  is the average time spent below the surface (i.e. ‘deep-  
 475 diving’), and  $t$  is the window of time during which an animal is within the visual range of an observer. A range  
 476 of estimates for the values of  $s$  and  $d$  were made based mainly on observational data from experienced humpback  
 477 whale scientists familiar with ‘Australian’ whales. A histogram of forward and aft distances was used to gain an  
 478 idea of the time window,  $t$ . Ignoring the fact that two aircraft with rather different fields of view were employed  
 479 on the 2008 survey, a similar histogram of distances to sighted pods is given in Figure 8. This suggests that a  
 480 maximum sighting ‘window’ can be estimated as about 8.5km, comprising animals seen ahead (generally up to  
 481 5.0km), abeam, and aft (up to 3.5km). These data suggest a rectangular sighting window of about 4.5km  
 482 (estimated from a half-normal model). The focal follow data collected during the 2008 land-based survey were  
 483 used to provide estimates of  $s$  and  $d$  of 405s and 246s (see Table 4). Average speed during the aerial survey was  
 484 132knots (244km/h). An estimate of  $t$  for a window of 4.5km is 66s, giving an estimate of  $g(0)$  of 0.72 – again,  
 485 much higher than from previous analyses. Estimates from this approach are fairly insensitive to quite large  
 486 changes in window-width (for example values of  $g(0)$  of 0.68 and 0.81 result from windows of 2.5km and  
 487 8.5km). The estimate of 0.72 is higher than those in the upper row of Table 5 (0.63 and 0.60) – i.e. those  
 488 computed when sightings from the land-based survey with no offshore distance recorded were excluded. The  
 489 former does not account for perception bias, however, so it would be expected to be higher than estimates from  
 490 the combined survey approach which do.

491 [Figure 8 about here]

492

493 The  $g(0)$  estimates in the bottom half of Table 5 are some 40-50% lower than those in the upper half, but are  
 494 more in line with our *a priori* expectation. These estimates are derived from land-based estimates which included  
 495 sightings for which no offshore distance was recorded. This would most certainly mean that ‘too many’ pods  
 496 were included in the land counts, especially since one of the main reasons for a missing offshore distance was  
 497 difficulty in acquiring two theodolite fixes of the same pod. Even beyond 8km, whales were sighted on the  
 498 horizon. Therefore at least some of the pods with missing distances would be expected to be within 12km  
 499 offshore.

500 A second objective of the 2008 survey was to compare results with the 1999 and 2005 surveys. Previous  
 501 analyses had estimated relative abundance of whales over a similar migration period to that assumed here as  
 502 3,441 for 1999 (Bannister and Hedley, 2001) and about  $22,500 \times 0.268 = 6,030$  for 2005 (Paxton *et al.*, in press;  
 503 Table 2, results set 13) – an estimated increase rate of 9.8% per annum. The estimate of 11,100 presented here  
 504 would represent an implausible rate of increase of 13.9% from the 1999 estimate; this rate is even more  
 505 implausible were it based on only the 2005 estimate. Paxton *et al.* (in press) retrospectively applied a correction  
 506 from their paper to the 1999 estimate to estimate absolute abundance of northward-migrating humpback whales  
 507 as 11,500 (95% CI 9,200-14,300) which fell within the range of 8,207-13,640 broadly estimated by Bannister  
 508 and Hedley. This compares with 22,500 (10,000 – 72,200) from the 2005 survey. (Note: The estimate of 22,500  
 509 was not considered the ‘best’ estimate of abundance by Paxton *et al.* (in press) since they considered that  
 510 extrapolation beyond the last flight of the aerial survey was unreliable due to a presumed ‘second pulse’ in the  
 511 migration curve. It is used in the comparisons here as the estimate which best corresponds temporally to the 1999  
 512 and 2008 migration periods.) The corresponding estimates from the present analysis are 17,500 (14,130-25,980)  
 513 or 33,850 (27,340-50,260). The latter represents an estimated rate of increase of about 12.7% (CV=0.19) given  
 514 an estimate of 11,500 in 1999, or about 14.6% (CV=0.53) given an estimate of 22,500 in 2005. Given the  
 515 conclusions of the Hobart Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback  
 516 Whales (IWC, 2006) that a rate of increase of 12.6% was biologically implausible, these estimates rates of  
 517 increase are implausibly high. It is our contention, however, that the analysis in this paper is sufficiently robust

518 that the point estimates of abundance obtained for the 2008 survey are reasonable. Clearly an infeasibly high rate  
 519 of increase can result from initial abundance estimates being too low, as well as current estimates being too high.

520 Separate from the  $g(0)$  estimation issue, is the question of the robustness of the estimates obtained from spatial  
 521 modelling of the aerial survey data. Therefore, as a sensitivity test to the spatial modelling approach adopted for  
 522 analysing these data, we compared the spatial modelling estimates (uncorrected for rate of passage and for  $g(0)$ )  
 523 to those from a conventional line transect analysis in *Distance* (Thomas *et al.*, 2010). Data used in the spatial  
 524 modelling included all on-effort data; only data from the main E-W transects were used in the design-based line  
 525 transect analysis (as was done previously (Bannister and Hedley, 2005; Paxton *et al.* (in press; results sets 5 and  
 526 6). The results are shown in Figure 9. It can be seen that the estimates from the spatial model are quite  
 527 comparable to those from a standard line transect analysis, the main difference being that variation in encounter  
 528 rate has been ‘smoothed’ out, as would be expected. Thus, there is no suggestion of anything untoward in the  
 529 relative estimates presented in Table 5.

530 [Figure 9 about here]

531

532 In conclusion, we propose that the best estimate for NM whales from the 2008 survey is 33,850 (27,340-50,260).  
 533 The caveat to this is that some of the land-based sightings from which the estimate of  $g(0)$  was derived would have  
 534 been beyond the truncation distance of 12km offshore, so the analysis is not strictly consistent. However,  
 535 a  $\hat{g}(0)$  of 0.33 is perhaps rather more plausible than the alternative of 0.63 when those sightings were excluded.  
 536 On the other hand, the higher  $\hat{g}(0)$  is compatible with the estimate obtained by directly estimating surface  
 537 availability (Barlow *et al.*, 1988). Since focal follow data were collected on this survey to estimate surfacing and  
 538 diving times directly, there appears to be no obvious reason to discount these higher estimates, other than they  
 539 are much higher than those obtained on previous aerial surveys. Therefore, we would also advocate a  
 540 conservative estimate of 17,500 (14,130-25,980) for this population, until these issues have been resolved.

541 A similar argument applies for the estimates of NM+ whales (Table 5). When a proportion of unknown-direction  
 542 pods are included in the analysis, the abundance estimates increase (by about 23% in the case of relative  
 543 abundance) compared to the corresponding NM estimates. These estimates are presented here as a sensitivity to  
 544 the main NM analysis, for which comparisons across the three surveys are currently more reliable.

545

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564

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609 **APPENDIX: VARIANCE PROPAGATION IN LINE TRANSECT SPATIAL MODELS**

610

611 A detection function,  $g(y; \pi)$ , is estimated from some line transect data,  $y$ , using some parameter estimates,  $\hat{\pi}_y$ .  
 612 The results are used to compute effective strip width (and hence  $\log(\text{effective area})$ ) along the tracklines, and  
 613 then  $\log(\text{effective area})$  is included in the spatial model of number of sightings per segment as an offset.  
 614 Integration over the fitted surface gives total abundance, but uncertainty in  $\hat{\pi}_y$  needs to be propagated through to  
 615 the final abundance estimate in order to estimate the variance in the abundance estimate.

616 Consider the  $i^{\text{th}}$  stretch of effort: suppose  $n_i$  whales were seen, and that the mean location of the segment was  
 617  $(lat_i, lon_i)$ . Denoting effective area by  $a_i$  and using a spatial smooth  $s(\cdot)$  to describe spatial abundance, we have

$$\begin{aligned} \log[E(n_i)] &= \log(a_i) + s(lat_i, lon_i) \\ &= l_i(\pi) + s(lat_i, lon_i) \\ &= l_i(\hat{\pi}_y + \delta) + X_i\beta \\ &\approx l_i(\hat{\pi}_y) + \left[ \frac{dl_i}{d\pi} \right]_{\pi=\hat{\pi}_y} \cdot \delta + X_i\beta \end{aligned}$$

618

619 where  $l_i = \log(a_i)$ ,  $\delta$  is defined as  $(\hat{\pi}_y - \pi)$ , and  $X$  is the design matrix associated with the smoother. Now note  
 620 that  $\left[ \frac{dl_i}{d\pi} \right] \delta$  and  $X_i\beta$  have identical ‘shape’ – they are both matrices dotted with vectors. The matrix of first  
 621 derivatives may be thought of as another ‘design matrix’ and  $\delta$  as a vector of unknown parameters. The prior  
 622 distribution of  $\delta$  has mean 0 and variance  $-H_\pi^{-1}$ , where  $H_\pi$  is the Hessian from maximizing the likelihood of  
 623 the detection function from the line transect data. The form of the prior distribution for  $\beta$  is also known; it is  
 624 Gaussian with mean 0 and variance  $\theta S^{-1}$ , where  $S$  is the penalty matrix and  $\theta$  is the smoothing parameter(s) (to be  
 625 estimated). Thus,  $\delta$  and  $\beta$  play very similar roles, the only difference being that the ‘smoothing parameter’ for  $\delta$   
 626 is known (it equals one), whereas for  $\beta$ , it needs to be estimated.

627