

BAYESIAN INFERENCE IN LINE TRANSECTS WITH DOUBLE COUNT SAMPLING AND IMPERFECT ON-LINE DETECTION

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■ **ABSTRACT:** *For the management and conservation of wild animal populations it is fundamental to know its abundance. However, if imperfect detection, a very common phenomenon in field counts, is ignored, abundance will be underestimated. We show that Bayesian hierarchical models for double observer distance sampling data are capable of simultaneously estimating abundance and detection probabilities and propose a simple model where detection probabilities are modeled as logit or probit regressions of distance-to-line and give its implementation in BUGS code. With a simulation study we verify empirically that double observer information increases the precision in abundance estimates by about 30% when compared with estimates from distance data only. We further verify that the model is capable to correctly estimate observer-specific detection probability, but underestimates abundance by 12% on average. We also apply an extension of these models to a population of loon (QUANG and BECKER, 1997; URL:<http://www.jstor.org/stable/1400405.1997>). Our estimate of 154 (posterior mean) was much higher than the estimated 99 individuals reported by QB although other model parameters are similar. Some new model-specific goodness-of-fit diagnostics are proposed and applied.*

■ **KEYWORDS:** *Animals distribution; ecological modeling; state process; observation model.*

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1 Introduction

The absolute size of an animal population is important to evaluate its conservation status and to monitor the sustainability of management actions. However, the estimation of abundance is often a difficult and expensive task, particularly in the marine environment. This is due to the extensive area of distribution and the elusiveness of individuals or groups who remain submersed. Marsh and Sinclair (1989) propose two sources of bias in abundance estimates, denoting them as availability and perception biases. Availability bias refers to the uncertain presence of the animal within the searched area at time of survey, while perception bias is caused by imperfect detection of animals or groups which are available.

Transect line distance sampling analysis (distance sampling, for short) is a commonly used method of estimating density and abundance for a variety of marine mammal populations, usually for the purpose of management and conservation (BORCHERS, BUCKLAND and ZUCCHINI, 2002; DALLA ROSA, FORD and TRITES, 2012). Data are collected by an observer travelling along prespecified routes (the transect line) while recording the perpendicular distances to the detected animals. If the animals occur in groups or clusters, such as flocks of birds or schools of dolphins, the number of animals in each group is recorded along with the distance to the groups centroid. Since some animals are missed (perception bias), approaches are needed to correct for it. This is achieved by modeling the probability of detection as a known function $g(\cdot)$ of perpendicular distance x , usually assuming that higher distances associate with lower detection probabilities. In order to have identifiable parameters, this function needs to assume perfect detection at some known distance. Conventional distance sampling assumes perfect detection on the transect line, $g(0) = 1$. If this assumption is violated (i.e. $g(0) < 1$), we say there is imperfect on-line detection and denote $1 - g(0)$ as perception bias. This feature is common for marine mammals and if unaccounted for will cause a downward bias in abundance estimates (BORCHERS, 1999; BORCHERS, BUCKLAND and ZUCCHINI, 2002).

Extensions of distance sampling to incorporate imperfect detection on the transect line as another parameter and guarantee parameter identifiability rely on double observer distance sampling with mark-recapture data between them (KARUNAMUNI and QUINN, 1995; LAAKE, 1999). These findings have been confirmed and extended by many other studies of various authors (QUANG and BECKER, 1996, 1997, 1998; BAILEY, HINES and MacKENZIE, 2007; CONN, LAAKE and JOHNSON, 2012; EGUCHI and GERRODETTE, 2009; ROYLE and DORAZIO, 2008).

Bayesian analysis has become increasingly popular in statistical inference of wildlife population abundance and related parameter (KARUNAMUNI and QUINN, 1995; BERLINER, 1996; WADE, 2000; DURBAN et al., 2005; McCARTHY, 2007; KING and BROOKS, 2008). Unlike the orthodox, more restrictive, definition of frequentist probability, a Bayesian probability is a much

broader metric capable to quantify any kind of uncertainty caused by incomplete information (JAYNES, 2003). Hence, a Bayesian population abundance estimate is given in the form of a (posterior) probability distribution. The Bayesian approach is further capable to combine available extra-data information (prior distributions) with new observed data (likelihood) to produce an updated state of information (posterior distributions) by way of Bayes theorem (KINAS and ANDRADE, 2010).

Hierarchical Bayesian models offer a flexible and realistic approach to ecological research (CLARK, 2005; SCHOFIELD and BARKER, 2010). Markov Chain Monte Carlo (MCMC) is a handy tool to obtain simulated high-dimensional posterior distributions with relative ease (MARTIN and QUINN, 2006; McCARTHY, 2007). Its implementation in BUGS code (LUNN et al., 2009; RESNIK and HARDISTY, 2010) with the use of specialized software (e.g. JAGS) (PLUMMER, 2003; PLUMMER, 2012) and related R libraries (rjags) (PLUMMER, 2013) have made Bayesian inference and hierarchical model fitting more accessible to applied scientist in general.

Bayesian hierarchical distance sampling models were sistematized by Royle and Dorazio, (2008, Chapter 7). In order to simulate the joint posterior distribution for all unknown parameters using MCMC, they formulate the model within a data augmentation framework providing a flexible structure to fit very general models (ROYLE and DORAZIO, 2008, P.181).

The aim of this paper is to formulate simple Bayesian hierarchical models implemented in BUGS code to estimate population abundance without assuming perfect detection on the transect line. Double observer distance sampling data are the basic requirements. Firstly, with the help of a simulated study we examine the reliability of the proposed hierarchical model to estimates abundance and imperfect on-line detection probability. Secondly, we explore further flexibilities of hierarchical model formulation with a case study on double observer distance data for a loon population in Alaska (QUANG and BECKER, 1997) in which we allow for maximum detection probability to occur off the transect line and evaluate the goodness-of-fit for these models with some novel diagnostic tools.

2 Method

2.1 The models

The models are formulated within a hierarchical structure and implemented with data augmentation (ROYLE and DORAZIO, 2008, P.181). The idea behind data augmentation is that the actual population of unknown size N is contained in a super-population of given size M assumed much larger than N .

Considering just distance data, we define a binary variable y_i which indicates whether the i -th subject has been detected ($y_i = 1$) or not ($y_i = 0$) for $i = 1, \dots, M$. The variable y_i has therefore a Bernoulli distribution with parameter μ_i . We express this distribution as

$$y_i \sim \text{Bernoulli}(\mu_i)$$

For each subject the parameter μ_i has two components: the detection probability $g(x_i)$, a function of the perpendicular distance to the transect line x_i , and the binary variable w_i , indicating whether the i -th subject, in the "augmented population" of known size M is part of the "real population" of unknown size N . For all detected animals $w_i = 1$ while it is unknown (or latent) for the remaining $M - n$ elements and has to be estimated. Hence, μ_i is defined as $\mu_i = w_i \cdot g(x_i)$ and w_i are independent Bernoulli random variables with success probability $\psi = N \cdot M^{-1}$ and therefore expressed as

$$w_i \sim \text{Bernoulli}(\psi)$$

Consequently it results that the sum $S_w = \sum(w_i)$, has a Binomial distribution $\text{Bin}(M, \psi)$. Hence, estimating N is equivalent to estimate ψ since $E(S_w) = M \cdot \psi = N$.

For perpendicular distances x [$0 \leq x \leq m$], where m is some fixed maximum perpendicular distance, we define de distance-dependent detection probability $g(x)$ with the inverse logit link function

$$g(x) = \frac{e^{(\beta_0 + \beta_1 \cdot x)}}{1 + e^{(\beta_0 + \beta_1 \cdot x)}}$$

and the inverse probit link function

$$g(x) = \Phi(\beta_0 + \beta_1 \cdot x)$$

where Φ is the standard Normal distribution function.

The detection probability on the transect line (i.e. $g(0)$) becomes a function of β_0 only for both link functions. Hence, by estimating β_0 we are estimating a known function of the perception bias $1 - g(0)$. When only distance data are available, β_0 is confounded with abundance and cannot be estimated individually. One way to circumvent this difficulty is the incorporation of mark-recapture information for two observers who simultaneously search the transect line and collect distance data individually (BUCKLAND, LAAKE and BORCHERS, 2010).

With the inclusion of the double observers (DO) information, the binary variable y_i extends to y_{ji} for observer j where $j = 1, 2$ and the detection probability becomes also observer-dependent $g_j(x_i)$. Variable y_{ji} is now associated with the indicator vector $Z_i = (z_{1i}, z_{2i}, z_{3i}, z_{4i})$, defined such that just one element is equal to one and all others are zeros. Thus, by $z_{1i} = 1$ we mean that the detection is just by observer 1 (i.e. $y_{1i} = 1$ and $y_{2i} = 0$) and the associated vector is $Z_i = (1, 0, 0, 0)$; when $z_{2i} = 1$ the detection is just by observer 2 and $Z_i = (0, 1, 0, 0)$; when $z_{3i} = 1$, the detection is by both observers and $Z_i = (0, 0, 1, 0)$; finally, $z_{4i} = 1$ and $Z_i = (0, 0, 0, 1)$ for all $M - n$ undetected subjects.

We consider that detections are independent between observers (i.e. $g_j(x_i) = g_{j|(3-j)}(x_i)$) with the right-hand side denoting the conditional probability that

observer j detects subject i given that the other observer also detects it). Thus, the probabilities of the four components of Z_i are easily calculated and the Binomial model for y_i is extended to a Multinomial model for Z_i with the following parameter structure:

$$\begin{aligned} Z_i &\sim \text{Multinomial}(1, (\mu_{1i}, \mu_{2i}, \mu_{3i}, \mu_{4i})) \\ \mu_{1i} &= g_1(x_i) \cdot (1 - g_2(x_i)) \cdot w_i \\ \mu_{2i} &= (1 - g_1(x_i)) \cdot g_2(x_i) \cdot w_i \\ \mu_{3i} &= g_1(x_i) \cdot g_2(x_i) \cdot w_i \\ \mu_{4i} &= 1 - (\mu_{1i} + \mu_{2i} + \mu_{3i}) \\ w_i &\sim \text{Bernoulli}(\psi) \end{aligned}$$

where $\text{Multinomial}(s, (p_1, \dots, p_k))$ denotes a k -dimensional multinomial distribution with sample size s and probability vector (p_1, \dots, p_k) satisfying $\sum p_r = 1$.

Finally, based on the n sampled detections with known distances x_i and the $M - n$ undetected augmented data the estimated population abundance becomes

$$N = \sum_{i=1}^M w_i = n + \sum_{i=n+1}^M w_i$$

For the $M - n$ undetected subjects with missing perpendicular distances x_i , these distances are assumed uniformly distributed in the interval $(0, m)$ and imputed.

2.2 The data

For the simulation study, we consider a virtual population of size $N = 200$ subjects, whose perpendicular distances to the transect line x , are independent random variable with uniform distribution in the interval $[0, 1]$. Any distance d , effectively measured in the field until some maximum fixed distance m , can always be standardized such that $x = d \cdot m^{-1}$ is in the range $[0, 1]$. Hence, there is no loss of generality by using this distribution. To generate the data we also define half-Normal detection functions $g_j(x_i) = k_j \cdot \exp(-x^2 \sigma_j^{-2})$ with parameters $k_1 = 0.8$; $\sigma_1 = 8$, for observer one and $k_2 = 0.5$; $\sigma_2 = 12$ for observer two. The detection of the i -th individual by observer j is modeled with a Bernoulli distribution $y_{ji} \sim \text{Bern}(g_j(x_i))$, where each individual i is classified as detected ($y_{ji} = 1$) or undetected ($y_{ji} = 0$) by observer j . The components of the vector Z_i for $i = 1, \dots, N$ are defined for the i -th individual as follows:

$$\begin{aligned} z_{1i} &= y_{1i} \cdot (1 - y_{2i}) \\ z_{2i} &= (1 - y_{1i}) \cdot y_{2i} \\ z_{3i} &= y_{1i} \cdot y_{2i} \\ z_{4i} &= (1 - y_{1i}) \cdot (1 - y_{2i}) \end{aligned}$$

A simulated sample consists in the distances x_i and associated vectors (z_{1i}, z_{2i}, z_{3i}) for a total $n = \sum_{i=1}^N (z_{1i} + z_{2i} + z_{3i})$ detected subjects. The full sampling procedure is replicated 20 times, each identified as transect t_r , where $r = 1, 2, \dots, 20$. The observed perpendicular distances and the total number of detected subjects are summarized and displayed in Figura 1.

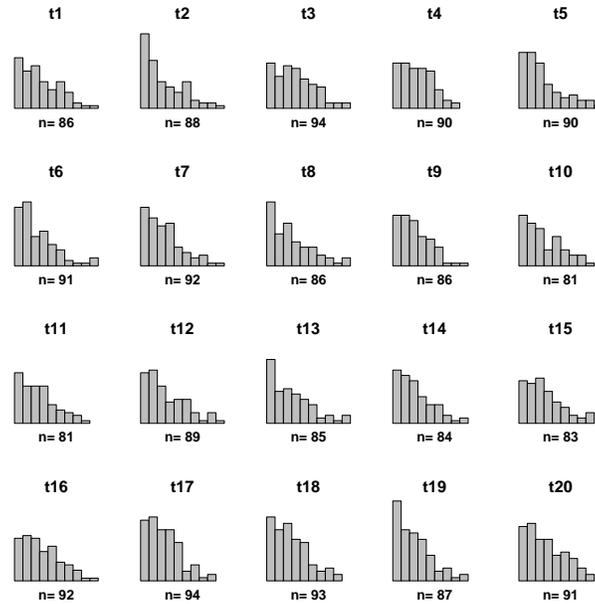


Figure 1 - Histogram of individual distances and total sample size n for 20 replicated samples extracted from the simulated population. All the frequencies (y -coordinates) are on the same scale and distances (x -coordinates) are on the interval $[0, 1]$.

The second data set is adapted from Quang and Becker (1997) and consists of a mixed population with two species of loons (*Gavia pacifica* and *Gavia immer*) inhabiting the Yukon Flats National Park, Alaska. Since double count distance data were reported only in interval classes (Table 1), we simulated within each class, the individual distances with uniform distributions.

Table 1 - Loon detection data reproduced from Quang and Becker (1997), Table 01

Distance class	5-30	30-60	60-90	90-120	120-150	150-190	190-250
Front passenger only	3	1	2	3	3	5	5
Rear passenger only	4	3	0	3	5	1	2
Both passengers	0	1	2	10	6	6	2

2.3 Fitted model

Models used for inference are distinct regarding data type and link function. In some models, data are only perpendicular distances to the line transect (LT); in others, double observer mark-recapture data are also included (DOLT). The link functions are logit or probit. From now on we will just use model numbers in Table 2 when referring to them. From now on we will use the shorthand 'DOLT-logit' when referring to the model fitted to double-observer distance data fitted with logit link; applying the obvious changes when referring to all other situations. In the case of LT models M1 and M2 we use the total number n of subjects detected by at least one observer and simply ignore capture-recapture information. This allows for the evaluation of changes in precision of abundance estimates obtained for the same sample size and distance data but including double observer data as well (M3 and M4).

Table 2 - List of models fitted to distance data only (LT) and complemented by double observer mark-recapture data (DOLT). The logit link is used in odd-numbered and the probit link in even-numbered models. The term *single* refers to models with a single detection function while *obs* refers to models with observer-specific detection functions. The term *quad* indicates the inclusion of a quadratic term ($p_{ji} = g_j(x_i)$)

Model	Description
M1 $\log\left[\frac{p_i}{(1-p_i)}\right] = \beta_0 + \beta_1 \cdot x_i$	<i>single LT – logit</i>
M2 $\Phi^{-1}(p_i) = \beta_0 + \beta_1 \cdot x_i$	<i>single LT – probit</i>
M3 $\log\left[\frac{p_{ji}}{(1-p_{ji})}\right] = \beta_0 + \beta_1 \cdot x_i$	<i>single DOLT – logit</i>
M4 $\Phi^{-1}(p_{ji}) = \beta_0 + \beta_1 \cdot x_i$	<i>single DOLT – probit</i>
M5 $\log\left[\frac{p_{ji}}{(1-p_{ji})}\right] = \beta_{j0} + \beta_{j1} \cdot x_i$	<i>double DOLT – logit</i>
M6 $\Phi^{-1}(p_{ji}) = \beta_{j0} + \beta_{j1} \cdot x_i$	<i>double DOLT – probit</i>
M7 $\log\left[\frac{p_{ji}}{(1-p_{ji})}\right] = \beta_0 + \beta_1 \cdot x_i + \beta_2 \cdot x_i^2$	<i>single quad DOLT – logit</i>
M8 $\Phi^{-1}(p_{ji}) = \beta_0 + \beta_1 \cdot x_i + \beta_2 \cdot x_i^2$	<i>single quad DOLT – probit</i>
M9 $\log\left[\frac{p_{ji}}{(1-p_{ji})}\right] = \beta_{j0} + \beta_{j1} \cdot x_i + \beta_{j2} \cdot x_i^2$	<i>double quad DOLT – logit</i>
M10 $\Phi^{-1}(p_{ji}) = \beta_{j0} + \beta_{j1} \cdot x_i + \beta_{j2} \cdot x_i^2$	<i>double quad DOLT – probit</i>

To fit the loon data, we further include a quadratic term of x to allow for the possibility of a maximum detection probability at some distance off the transect line ($x > 0$). To select the most parsimonious model we use the deviance information criterion (DIC), with smaller DIC meaning a better fit (SPIEGELHALTER et al., 2002). To facilitate later reference just by model number, all fitted models are listed in Table 2.

2.4 Bayesian inference - simulated data

Models 1 to 6 (Table 2) are fitted to each of the 20 replicated transects. We define vague marginal priors for all parameters: $\psi \sim U(0, 1)$; $\beta_{j0} \sim N(0, 1E5)$ and $\beta_{j1} \sim N(0, 1E5)$ to $j = 1, 2$. Posterior distributions are obtained by Markov Chain Monte Carlo (mcmc) simulations (MARTIN and QUINN, 2006; McCARTHY, 2007) with the libraries R2jags (SU and YAJIMA, 2015) and rjags (PLUMMER, 2013), which run JAGS (PLUMMER, 2003; PLUMMER, 2012) from within R (version 3.1.1) (R CORE TEAM, 2014).

We evaluate convergence with the diagnostic tools Rhat and n.eff provided by R2jags, in combination with the standard diagnostics provided in the 'coda' package (PLUMMER, 2010; PLUMMER, 2013). After some preliminary testing we have fixed the fitting procedure that achieved satisfactory convergence diagnostics, running three chains with a burn-in of 10.000 steps and a thinning of 40, generating a posterior sample of size 3000.

To assess inferential efficiency in estimating population size N and detection probability at maximum detection $g_j(0)$ we use the relative bias (rb) defined as the difference between the posterior mean and the true value divided by the true value. As a summary over the twenty replicates we further calculate the average rb and also the root mean squared error ($rmse$) among posterior means; where $rmse$ is defined as the variance of the posterior mean plus the squared difference between the average posterior mean and the true parameter.

2.5 Bayesian inference - loon data

Models 3 to 10 (Table 2) are fitted to the loon data with vague prior distributions for all model parameter: $\psi \sim U(0, 1)$; $\beta_{j0} \sim N(0, 1E5)$, $\beta_{j1} \sim N(0, 1E5)$ e $\beta_{j2} \sim N(0, 1E5)$. The posterior distributions are obtained as previously, with three chains, a burn-in of 10.000 steps and a thinning of 40, generating a posterior sample of size 3000. Preliminary testing indicated good convergence diagnostics when running mcmc with these options.

Models with an additional quadratic term β_2 (models 7 and 8) or the observer-specific extension β_{j2} (models 9 and 10) have the maximum detection probability at some positive perpendicular distance $x_0 > 0$. For some fixed values β_1 and β_2 this distance is:

$$x_0 = -\frac{\beta_1}{2\beta_2}$$

Therefore, in a quadratic model, $g(x_0)$ replaces $g(0)$ as the distance with maximum detection probability. Within the Bayesian framework, it is easy to obtain a posterior distribution for this probability, since it is a known function of the uncertain parameters β_0, β_1 and β_2 (or their j -indexed equivalents) for which joint posterior distribution is readily available. For the inverse-logit and inverse-probit link functions, these maximum detection probabilities are, respectively

$$g(x_0) = (1 + e^{-(\beta_0 - \frac{\beta_1^2}{4 \cdot \beta_2})})^{-1}$$

$$g(x_0) = \Phi(\beta_0 - \frac{\beta_1^2}{4 \cdot \beta_2})$$

For later reference, we mention that these maximum detection probabilities $g_j(x_0)$ are equivalent to the parameters c_j for observer $j = 1, 2$ in Quang and Becker (1997) defined in another very different model formulation.

2.6 Goodness-of-fit - loon data

The rationale to evaluate the quality of model fit is to check whether, with a proposed model and the resulting parameter estimates, we are able to generate predictive distributions consistent with the observed sample data (GELMAN and HILL, 2007, p.513). That is, to compare the observed total number of detections by the front passenger only ($n_{1o} = 22$), by the rear passenger only ($n_{2o} = 18$) and by both passengers ($n_{bo} = 27$), with the three-dimensional predictive distribution induced by the posterior distribution.

Based on the given perpendicular distances x_i ($i = 1, \dots, M$) in the augmented population of size M and given the posterior sample of size 3000 for the parameter vector $\theta_{(s)}$ ($s = 1, \dots, 3000$), which for the most general models (M9 and M10) is $\theta_{(s)} = (\psi_{(s)}, \beta_{j0(s)}, \beta_{j1(s)}, \beta_{j2(s)})$ ($j = 1, 2$) we repeat the steps describe next for each s .

Generate M random quantities $w_{i(s)}$ from the Bernoulli distribution with parameter $\psi_{(s)}$. For each of the M subjects calculate the probability vector $\mu_{i(s)} = (\mu_{1i(s)}, \mu_{2i(s)}, \mu_{3i(s)}, \mu_{4i(s)})$ and simulate $Z_{i(s)} = (z_{1i(s)}, z_{2i(s)}, z_{3i(s)}, z_{4i(s)})$ from a multinomial distribution of size one and parameter $\mu_{i(s)}$. Obtain the sums $n_{r(s)} = \sum_{i=1}^M z_{ri(s)}$ for $r = 1, 2, 3$ which are the predicted numbers of subjects detected by observer one only ($n_{1(s)}$), observer two only ($n_{2(s)}$) and by both ($n_{3(s)}$). Hence, the predicted total sample size is $n_{(s)} = n_{1(s)} + n_{2(s)} + n_{3(s)}$.

The procedure outlined in the previous paragraph, is repeated for all 3000 simulated posterior parameter vectors $\theta_{(s)}$ to generate a predictive distributions to be confronted with observed mark-recapture data. A model with adequate fit is expected to display predictive distributions in line with actual observations.

Finally, two further model checks are used: (i) the empirical cumulative distribution function (ecdf) of observed distances is compared to ecdf-s build from predicted observed distances simulated for posterior parameter vectors $\theta_{(s)}$; (ii) the observed sample size is compared to sample sizes of the posterior predicted samples,

3 Results

3.1 Simulated data

All models were fitted with the logit and the probit links. However, based on *DIC* no link provides a uniformly superior fit. Therefore, we focus the description

below only on the logit link, but retain in Tables and Figures the results for both.

Abundance estimation with distance data only (M1) has an average posterior standard deviation of 68, which reduces to an average of 31 when double observer data are included and a single detection function is assumed (M3) and reduces still further to 21 when observer-specific detection functions are assumed (M5)(Table 3a). However, using the posterior means of the 20 replicas we observe (*rb*) that models M1 and M3 are positively biased by 9% of the true value while model M5 is biased negatively by about 12% (Table 3a and 3b). A compromise between bias and precision is best described by the root mean square error (*rmse*) calculated over the replicated posterior means (Table 4). Based on the smallest *rmse* (33.76) model M5 is the best among these three models. Finally, regarding the coverage provided by the posterior 95% credibility intervals (CrI95), the true parameter N was covered by 16 out of 20 replicas for both DOLT models M3 and M5 (Figura 2). This coverage is below the 19 out of 20 as announced by the credibility interval.

Abundance estimate to modelos front M1 to M6

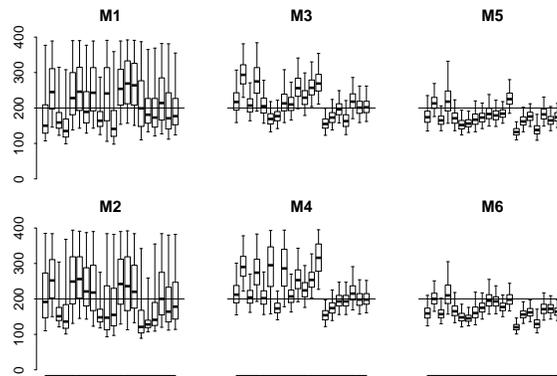


Figure 2 - Box-plot-type posterior distribution summaries of abundance (N) for models M1 to M6. CrI50 (boxes), CrI95 (whiskers), median (inbox horizontal line), true parameter (horizontal line).

Model comparisons with *DIC* consistently identified the model with observer-specific detection function M5 as better (i.e. lower *DIC*) than the model that assumes a single detection curve M3 (Table 3a and 3b). This consistency also holds for models with probit link (i.e., M6 is better than M4).

Table 3 - (a) Posterior means of abundance, (N); standard deviation, (sd); relative bias, (rb) and DIC. (b) Posterior means of $g(0)$; standard deviation (sd); relative bias (rb) for M1 to M4; and $g_1(0)$ and $g_2(0)$ for M5 and M6

	M1				M2				M3				M4				M5				M6						
	N	sd	rb	DIC	N	sd	rb																				
t1	180	74	-0.10	4226	214	81	0.07	4623	220	38	0.10	821	216	38	0.08	839	177	25	-0.12	665	161	22	-0.20	656			
t2	255	71	0.28	2696	258	67	0.29	2454	296	39	0.48	1113	293	40	0.47	1180	216	24	0.08	1005	202	22	0.01	953			
t3	172	45	-0.14	2376	165	45	-0.17	2550	209	28	0.05	1013	207	28	0.04	1023	167	17	-0.17	837	159	18	-0.20	948			
t4	153	53	-0.23	3480	165	72	-0.17	5477	279	51	0.40	1194	278	50	0.39	1156	224	44	0.12	1303	216	39	0.08	1184			
t5	243	74	0.21	3314	254	78	0.27	3384	208	31	0.04	992	206	31	0.03	984	173	23	-0.13	927	168	21	-0.16	892			
t6	255	73	0.27	3051	261	72	0.31	2831	170	22	-0.15	772	289	69	0.44	738	154	18	-0.23	749	149	16	-0.25	704			
t7	210	68	0.05	3520	238	70	0.19	3259	178	20	-0.11	771	175	20	-0.12	787	158	15	-0.21	708	146	14	-0.27	679			
t8	253	74	0.27	2813	234	80	0.17	3745	219	38	0.09	1151	288	63	0.44	996	170	23	-0.15	908	164	25	-0.18	1021			
t9	175	41	-0.13	1719	160	40	-0.20	2030	213	27	0.06	888	209	27	0.05	878	174	19	-0.13	816	176	19	-0.12	800			
t10	242	86	0.21	3820	183	88	-0.09	6060	260	38	0.30	1150	257	38	0.29	1192	186	23	-0.07	1045	198	25	-0.01	1063			
t11	168	70	-0.16	3895	188	84	-0.06	4854	231	31	0.16	1005	227	30	0.14	1001	181	19	-0.10	863	194	20	-0.03	825			
t12	260	65	0.30	2220	250	77	0.25	3453	259	32	0.30	815	256	32	0.28	827	185	16	-0.08	623	178	16	-0.11	635			
t13	273	70	0.36	2178	243	85	0.22	3935	273	36	0.36	990	316	48	0.58	922	227	24	0.13	882	200	20	-0.00	862			
t14	267	71	0.34	2242	236	74	0.18	3026	157	20	-0.22	608	155	19	-0.23	614	133	13	-0.33	492	121	11	-0.40	483			
t15	217	82	0.09	4014	149	67	-0.26	5007	175	22	-0.13	784	176	22	-0.12	804	164	18	-0.18	708	157	16	-0.21	650			
t16	201	61	0.00	2981	138	36	-0.31	2220	198	23	-0.01	722	195	23	-0.02	799	177	17	-0.12	658	164	16	-0.18	665			
t17	195	67	-0.02	3781	170	67	-0.15	5202	166	25	-0.17	720	164	26	-0.18	766	140	19	-0.30	673	131	17	-0.34	653			
t18	228	74	0.14	4000	220	79	0.10	4838	221	31	0.11	941	219	31	0.10	973	184	22	-0.08	857	173	20	-0.13	839			
t19	198	76	-0.01	4148	193	75	-0.04	4646	204	26	0.02	798	200	25	0.00	784	166	17	-0.17	670	173	17	-0.13	630			
t20	197	61	-0.01	3230	203	77	0.02	4893	205	25	0.02	877	201	23	0.00	838	175	18	-0.12	771	165	15	-0.18	709			
mean	197	68	0.09	3185	206	71	0.03	3924	217	31	0.09	909	226	34	0.13	905	176	21	-0.12	808	170	19	-0.15	793			

	M3				M4				M5				M6											
	$g(0)$	sd	rb	DIC	$g(0)$	sd	rb	DIC	$g_1(0)$	sd	rb	DIC	$g_2(0)$	sd	rb	DIC	$g_1(0)$	sd	rb	DIC	$g_2(0)$	sd	rb	DIC
t1	0.62	0.08	-0.046	0.59	0.08	-0.095	0.88	0.88	0.06	0.42	0.08	0.42	0.08	0.07	0.097	0.88	0.07	0.097	0.88	0.07	0.097	0.41	0.09	-0.175
t2	0.60	0.07	-0.071	0.57	0.07	-0.116	0.84	0.84	0.06	0.45	0.08	0.45	0.08	0.06	-0.105	0.84	0.07	0.051	0.84	0.07	0.051	0.44	0.08	-0.123
t3	0.66	0.07	0.019	0.65	0.07	-0.002	0.83	0.83	0.07	0.038	0.50	0.09	-0.004	0.81	0.08	0.81	0.08	0.010	0.81	0.08	0.010	0.47	0.09	-0.067
t4	0.46	0.09	-0.298	0.44	0.08	-0.326	0.66	0.66	0.11	-0.172	0.30	0.08	-0.397	0.65	0.11	-0.192	0.65	0.09	-0.192	0.65	0.09	0.32	0.08	-0.365
t5	0.64	0.07	-0.021	0.62	0.08	-0.046	0.74	0.74	0.09	-0.079	0.51	0.09	0.029	0.73	0.09	0.73	0.09	-0.087	0.73	0.09	-0.087	0.50	0.09	0.008
t6	0.73	0.06	0.127	0.53	0.48	-0.182	0.78	0.78	0.07	-0.027	0.68	0.08	0.361	0.78	0.07	0.78	0.07	-0.031	0.78	0.07	-0.031	0.67	0.08	0.340
t7	0.76	0.06	0.163	0.75	0.06	0.147	0.91	0.91	0.05	0.133	0.60	0.08	0.209	0.91	0.05	0.91	0.05	0.133	0.91	0.05	0.133	0.59	0.08	0.178
t8	0.56	0.08	-0.144	0.54	0.40	-0.177	0.84	0.84	0.08	0.046	0.38	0.08	-0.238	0.82	0.09	0.82	0.09	0.028	0.82	0.09	0.028	0.37	0.08	-0.255
t9	0.71	0.06	0.090	0.70	0.06	0.078	0.77	0.77	0.07	-0.032	0.63	0.08	0.257	0.77	0.07	0.77	0.07	-0.032	0.77	0.07	-0.032	0.62	0.08	0.248
t10	0.59	0.07	-0.088	0.57	0.07	-0.123	0.77	0.77	0.08	-0.041	0.41	0.08	-0.180	0.77	0.08	0.77	0.08	-0.042	0.77	0.08	-0.042	0.41	0.08	-0.180
t11	0.67	0.07	0.030	0.65	0.07	0.003	0.85	0.85	0.06	0.064	0.51	0.08	0.022	0.84	0.06	0.84	0.06	0.054	0.84	0.06	0.054	0.50	0.08	0.008
t12	0.78	0.06	0.192	0.74	0.06	0.144	0.92	0.92	0.04	0.151	0.62	0.08	0.243	0.94	0.04	0.94	0.04	0.170	0.94	0.04	0.170	0.59	0.08	0.180
t13	0.70	0.06	0.081	0.62	0.38	-0.046	0.78	0.78	0.07	-0.030	0.63	0.08	0.254	0.76	0.07	0.76	0.07	-0.047	0.76	0.07	-0.047	0.61	0.08	0.230
t14	0.80	0.05	0.233	0.79	0.06	0.216	0.96	0.96	0.03	0.196	0.63	0.08	0.253	0.96	0.03	0.96	0.03	0.202	0.96	0.03	0.202	0.61	0.08	0.225
t15	0.73	0.07	0.124	0.72	0.07	0.109	0.90	0.90	0.05	0.121	0.59	0.09	0.181	0.90	0.06	0.90	0.06	0.124	0.90	0.06	0.124	0.59	0.09	0.179
t16	0.77	0.06	0.182	0.75	0.06	0.159	0.93	0.93	0.03	0.165	0.60	0.08	0.200	0.94	0.04	0.94	0.04	0.181	0.94	0.04	0.181	0.59	0.08	0.175
t17	0.69	0.08	0.057	0.67	0.08	0.031	0.83	0.83	0.08	0.039	0.57	0.10	0.137	0.82	0.09	0.82	0.09	0.024	0.82	0.09	0.024	0.55	0.10	0.107
t18	0.67	0.07	0.031	0.65	0.07	0.004	0.82	0.82	0.07	0.020	0.54	0.09	0.071	0.79	0.08	0.79	0.08	-0.008	0.79	0.08	-0.008	0.51	0.09	0.020
t19	0.75	0.06	0.153	0.73	0.06	0.123	0.89	0.89	0.05	0.108	0.63	0.08	0.259	0.89	0.05	0.89	0.05	0.113	0.89	0.05	0.113	0.63	0.08	0.259
t20	0.74	0.06	0.136	0.73	0.06	0.118	0.88	0.88	0.06	0.102	0.59	0.08	0.189	0.88	0.05	0.88	0.05	0.100	0.88	0.05	0.100	0.60	0.08	0.204
mean	0.68	0.07	0.047	0.65	0.12	0.001	0.84	0.84	0.06	0.047	0.54	0.08	0.079	0.83	0.07	0.83	0.07	0.042	0.83	0.07	0.042	0.53	0.08	0.060

In all *DOLT* models the estimates of $g(0)$ have a good performance. For the observer-specific model M5, these estimates have a positive bias of 5% and 8% for observers one and two, respectively (Table 3a and 3b). Hence, they are less biased than estimates of abundance described previously. Model M3, that assumes a single detection function is also quite able to estimate the average between the true values (0.8 and 0.5) for both observers, which is $g(0) = 0.65$ (Table 3a and 3b). Regarding coverage of the 95% credibility intervals, 17 and 18 out of 20 are the success rates for observers one and two in model M5 (Figure 3).

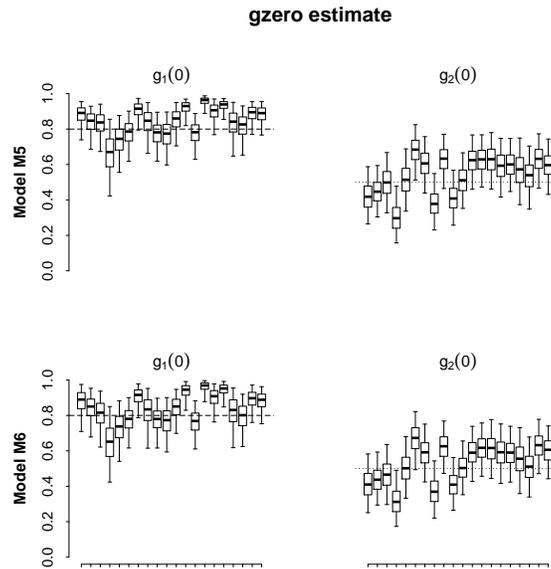


Figure 3 - Box-plot-type posterior distribution summaries of detection probability at distance zero for observer 1 ($g_1(0)$) and observer 2 ($g_2(0)$) for simulated data fitted to models M5 and M6. CrI50 (boxes), CrI95 (whiskers), median (inbox horizontal line), true parameter (dotted horizontal line).

3.2 Case study

All linear and quadratic *DOLT* models listed in Table 2 were fitted to the loon data; summaries are in Table 5. The models with smallest *DIC* are M8 and M10 which include a quadratic term for observed distances and uses the probit link. However, both models are indistinguishable regarding predictive performance, since *DIC*s differ only by one unit. In fact, differences in abundance estimates N are negligible since they have posterior mean 156 (CrI95: 128 to 189) and 154 (CrI95: 125 to 185) for models M8 and M10, respectively. Nevertheless, these estimates exceed in about 35% the estimated 99 individuals obtained by Quang and Becker (QB). For further comparisons with results by QB, we focus on model M10 which

retains observer-specific detection functions as they did.

In model M10 the observer-specific detection probabilities at distance zero ($g_1(0)$, $g_2(0)$) and the detection probabilities at the distances of maximum detection probabilities ($g_1(x_{10})$, $g_2(x_{20})$) are higher than the corresponding estimates reported by QB (Table 4; 5; Figura 4c and 4d). However, while posterior standard deviations in the former estimates are similar to the asymptotic standard errors (ASE) presented by QB, our values are much smaller for the latter where posterior standard deviation are close to 0.05 while the ASEs are above 0.25 (Table 4).

Table 4 - Summaries over 20 replicated simulations of the posterior mean for abundance N : average (mean); standard deviation among posterior means (sdpm); root mean square error (rmse) and average DIC among replicates (DIC_m)

	M1	M2	M3	M4	M5	M6
mean	217.264	206.169	217.003	226.419	176.464	169.809
sdpm	37.134	39.866	39.544	47.167	24.197	23.927
rmse	40.951	40.340	43.044	54.062	33.755	38.523
DIC_m	3185	3924	909	905	808	793

Table 5 - Posterior mean and sd for abundance (N); detection probability at distance zero for single detection function or for observer 1, ($g_1(0)$) and for observer 2, ($g_2(0)$); maximum detection probability at distance x_0 for single detection function or for observer 1, ($g_1(x_0)$) and for observer 2, ($g_2(x_0)$). Last line (QB) reproduces maximum likelihood estimates and asymptotic standard error from Quang and Becker (1997)

	N	sd	g1(0)	sd	g2(0)	sd	g1(x0)	sd	g2(x0)	sd	DIC
M3	84	7.38	0.440	0.124	-	-	-	-	-	-	477
M4	85	7.72	0.442	0.122	-	-	-	-	-	-	498
M5	82	6.84	0.396	0.091	0.531	0.096	-	-	-	-	453
M6	83	6.85	0.338	0.136	0.541	0.148	-	-	-	-	454
M7	144	14.11	0.224	0.056	-	-	0.852	0.040	-	-	278
M8	156	15.58	0.124	0.056	-	-	0.902	0.041	-	-	251
M9	141	14.19	0.202	0.068	0.302	0.103	0.876	0.052	0.932	0.052	287
M10	154	15.12	0.095	0.058	0.193	0.094	0.879	0.054	0.924	0.056	252
QB	99	6.34	0.110	0.080	0.162	0.089	0.754	0.256	0.732	0.283	-

Goodness-of-fit diagnostics suggest that model M10 is less capable of adequately predicting the observed number of mark-recapture data than the simpler model M6 (Figura 5 and 6). The graphic displays suggest that M10 predicts larger sample sizes of detected loon than the 67 individuals that were actually observed. Only with regard to the predicted distribution of distances (Figura 6) M10 seems to be slightly superior. This results are surprising because M10 has a much smaller DIC than M6 and therefore one would expect to observe features in support of a better fit.

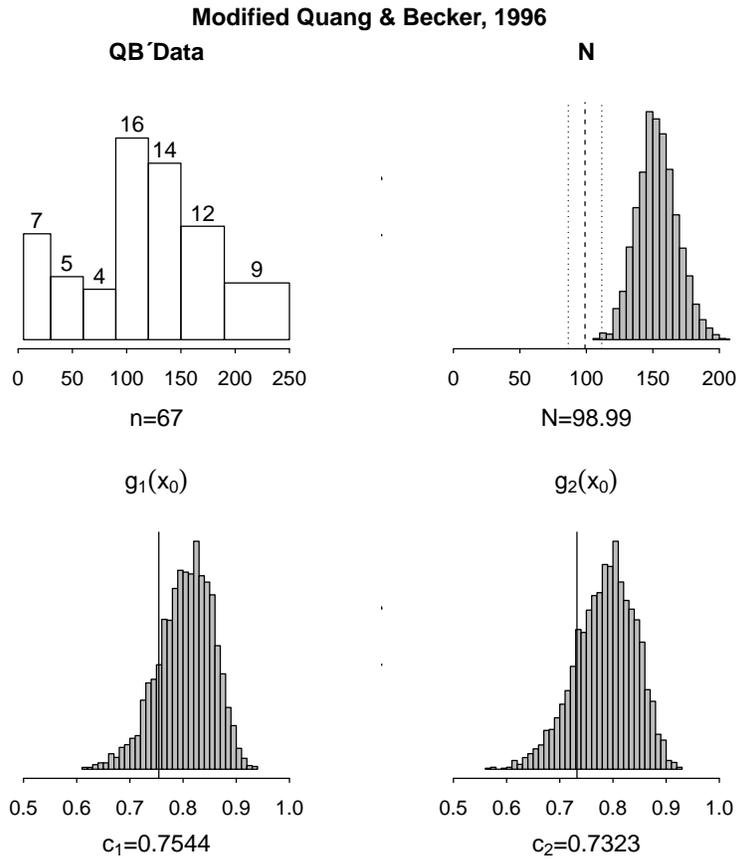


Figure 4 - Top left: histogram of observed data by QB; Top right: posterior distribution for abundance N and the corresponding estimate with confidence range by QB [vertical lines]; Bottom left: posterior distribution of highest detection probability for observer 1 [$g_1(x_0)$] and the estimate of this parameter (c_1) by QB [vertical line]; Bottom right: posterior distribution of highest detection probability for observer 2 [$g_2(x_0)$] and the estimate of this parameter (c_2) by QB [vertical line]. All posterior distributions refer to model M10.

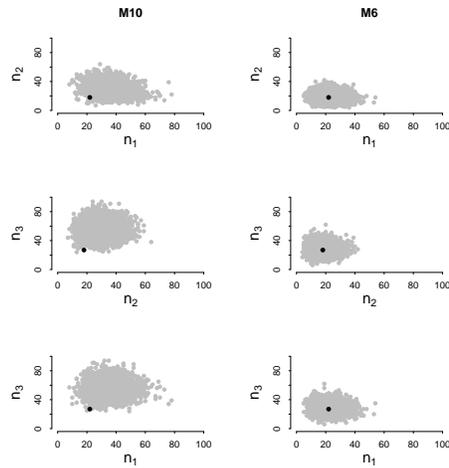


Figure 5 - Predictive multivariate distribution under models M10 (left column) and M6 (right column) [grey dots]. n_1 - number of individuals detected by observer one only; n_2 - by observer two only; n_3 - by both observers. The observed numbers (n_{1o}, n_{2o}, n_{3o}) are displayed with black dots.

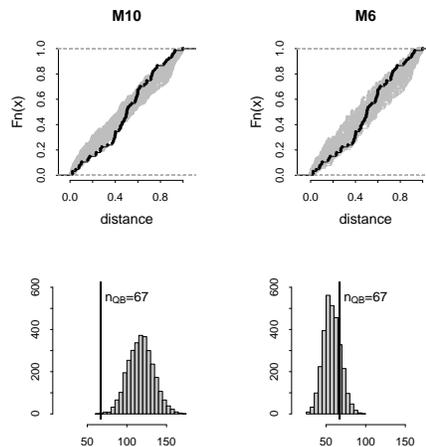


Figure 6 - Top row: A random sample of 16 empirical cumulative distribution functions (ecdf) [grey] of predicted distances and the observed ecdf [black]; Bottom row: predictive distribution of total number of detected loons [grey histogram] and observed number (67) [black vertical line]. Left column: M10 and Right column: M6.

4 Discussion

4.1 Simulated data

Our simulations confirm similar findings already reported by other authors that double observer mark-recapture data, when combined with perpendicular distances from the detected subject to the transect line, enables the estimation of $g(0)$ and increases the accuracy in abundance estimates (BORCHERS, 1999; KING, 2014). Hence, the double-observer data allowed for successful observer-specific estimation of the imperfect on-line detection probability $g(0)$ (Table 3b, Figura 3). The literature on distance sampling uses both terms $g(0)$ and perception bias ($1 - g(0)$) and some care is necessary when comparisons are intended. For instance, on-line detection probability of $g(0) = 0.8$ translates to a perception bias of 20%. Of course, perception bias is zero and can be ignored when $g(0) = 1$ as in standard distance sampling.

Furthermore, in standard distance sampling maximum detection is presumed to occur on the transect line ($x = 0$) and model with the shape of half-normal or hazard-rate detection functions (BORCHERS, BUKLAND and ZUCCHINI, 2002; FEWSTER et al., 2009; EDEKOVEN et al., 2013). But this maximum will be found at some positive distance $x_0 > 0$ when the detection function is assumed Weibull (QUANG and BECKER, 1997) or gamma (BECKER and QUANG, 2009). In contrast, we allow for an off transect line maximum detection simply by adding a quadratic term into de logit and probit regressions of distance. The important point in all this being that, with distance data only, parameter identifiability of detection functions in all these models are only possible when $g(x_0) = 1$ is assumed at some fixed $x_0 \geq 0$ (Z AHL, 1989).

In the simulation study the use of a logit or probit regression to model detection as a function of distance proved succesful although these were not the models that actually generated the data. With the chosen modeling strategy we took a quite distinct approach from most of the distance sampling literature (e.g. BORCHERS, 1999; BECKER and QUANG, 2009). To our knowledge, only Conn, Laake and Johnson (2013) used a somewhat similar modeling approach with a multivariate probit transformed detection function. However they used a much more complex reversible jump mcmc algorithm to obtain posterior distributions.

4.2 Case study

The inclusion of a quadratic term into the logit and probit regressions of detection probability by distance, resulted in a substantial reduction in DIC dropping from a smallest value of 454 for the best linear-term-only model M6 to 252 when a quadratic term was added (M10) (Table 5). This is not surprising since the data suggest a mode at some intermediate distance away from zero (Figura 4a). The posterior distributions obtained with model M10, estimate these modes at 140m (CrI95 123.2m to 163.5m) and 118m (CrI95 102.7m to 135.7m) for both observers. Using a completely distinct model structure and maximum likelihood

inference, QB estimates them at 135.05m and 122.82m respectively. In conventional distance sampling, the requirement of maximum detection on the transect line forces all distances smaller than the mode to be discarded and the remaining distances rescaled; a procedure usually known as data truncation (LAAKE, 1999; BORCHERS, BUCKLAND and ZUCCHINI, 2002; ANDRIOLO et al., 2010). This is unfortunate because it requires the exclusion of data that are often hard and expensive to collect.

Although the estimated distances of maximum detection x_0 show good agreement with QB, the estimated detection probabilities at these distances are lower in QB when compared to ours, although within acceptable ranges since both are covered by our posterior 95% credibility intervals (Table 4, Figura 4c and 4d). In contrast, abundance estimates cannot be reconciled as our posterior mean of 154 (CrI95 128 to 185) is much higher than the estimated 99 individuals reported by QB. It is surprising that, while QB infer a perception bias around 25% that is higher than our inferred value around 10%, their abundance estimate is smaller. This fact suggests that, with the inclusion of a quadratic term into our (probit- or logit-) regression models, the relationship between abundance and perception bias becomes less obvious than naive intuition would indicate. It is also to be noted that in all quadratic models the probit regressions (M8 and M10) outperform their logit equivalents (M7 and M9, respectively).

In the goodness-of-fit analysis we confronted the most complete quadratic model M10 to the most complete linear model M6. Based on posterior predictions, the visual examination of both Figures suggest that the observed number of detections was lower than model M10 would have predicted, being in better agreement with M6 (Figura 5 and 6). These findings contradict the ranking obtain by DIC, which might have been affected by missing distances induced by data augmentation (CELEUX et al, 2006). Finally, in Figura 7 we see that the detection probabilities estimated by M10 are reasonable in light of the data, while those for M6 are much less so and might be difficult to justify in practice. We think these aspects of model goodness-of-fit diagnostics need further investigation as it is unclear at this time how to reconcile these surprising results of lower DIC associated to worse lack-of-fit.

Finally, the simulation study has shown that the proposed model and its implementation with data augmentation in BUGS code, is a workable and comparatively easy way to model distance data with imperfect maximum detection probability. Furthermore, the case study has shown another versatility of this model by allowing for maximum detection off the transect line by simply including a quadratic term into the model. With this simple model extension, data loss due to truncation can be avoided. This can represent a critical advantage for elusive populations where samples are hard to get and each datum contains valuable information.

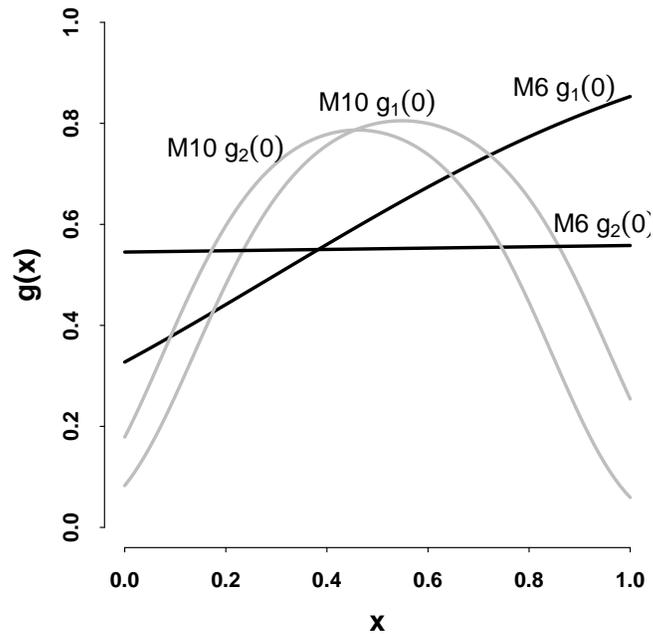


Figure 7 - Estimated detection functions for both observers under models M10 [grey] and M6 [black], when the probit regression parameters are fixed at the posterior means.

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GUILHERME-SILVEIRA, F. R.; KINAS, P. G. Inferência bayesiana para o método de transecção linear com dupla observação e detecção imperfeita sobre a linha de transecção. *Rev. Bras. Biom.*, Lavras, v.34, n.1, p.84-106, 2016..

■ RESUMO: Conhecer a abundância absoluta de populações animais é primordial para seu manejo e sua conservação. Porém, estimativas de abundância, que ignoram a detecção imperfeita dos indivíduos presentes nas áreas, resultam em subestimativas. Modelos hierárquicos com uma abordagem bayesiana, que fazem uso de dados de distâncias com a informação do segundo observador permitem estimar simultaneamente abundância e detectabilidade. Propomos uma alternativa de implementação simples, usando dados aumentados e simulação de Monte Carlo com Cadeia de Markov (mcmc). As probabilidades de detecção são modeladas por regressões logit e probit em função das distâncias aos indivíduos detectados. Validamos nossos modelos com amostras simuladas de uma população fictícia de tamanho conhecido e com funções de detectabilidade distintas. Implementamos novos recursos de diagnósticos para *goodness-of-fit* dos modelos aos dados. A complementação dos dados de distância com dados de um segundo observador, aumentou a precisão da estimativa de abundância em 29,6% com relação ao uso exclusivamente dos dados de distância. O melhor modelo, M5, estima corretamente os valores $g(0)$, porém a abundância é subestimada em 12% considerando-se a média da distribuição como estimativa pontual. Também aplicamos o modelo a uma população de gansos Loon descrita e analisada em Quang and Becker (1997). Nossa estimativa de 154 loons é maior que a estimativa de 99 indivíduos reportada em QB. O diagnóstico de *goodness-of-fit*, no entanto, indicam que o modelo é adequado. O estudo simulado sugere que a população seja ainda maior. Modelos hierárquicos integrando amostras de distância com dados de marcação e recaptura permitem estimar simultaneamente abundância e curvas de detecção. A modelagem das probabilidades de detecção por regressão logit ou probit, permite flexibilidade para ajuste de curvas não-convencionais com potencial para inclusão de outras covariáveis. Apesar da estimativa de curva de detectabilidade para ambos os observadores não ser o objetivo mais relevante do trabalho, os modelos propostos lidam com a problemática do viés de percepção de tal forma a fornecer uma estimativa de abundância com bastante precisão.

■ KEYWORDS: *Distribuição animal; modelagem ecológica; modelo de processo; modelo observacional.*

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