

## Short Communications

# A COMPARISON OF DIRECT AND DISTANCE SAMPLING METHODS TO ESTIMATE ABUNDANCE OF NESTING GULLS

## UNA COMPARACIÓN DE MÉTODOS DIRECTOS Y DE MUESTREO POR DISTANCIA PARA ESTIMAR LA ABUNDANCIA DE GAVIOTAS NIDIFICANTES

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**SUMMARY.**—We compared the performances of the strip transect count method and the distance sampling method during colony surveys of large gulls to estimate the total number of nests. Ten colonies were surveyed by both methods. Nest detection probabilities varied from  $0.519 \pm 0.064$  to  $0.706 \pm 0.049$  and the average nest detection probability was  $0.614 \pm 0.015$ . Nest densities were highly variable, ranging from 77 nests/ha to 717 nests/ha. Estimates of the number of nests obtained by the strip transect count method averaged 9.3% lower than those obtained by distance sampling but by as much as 31% in some colonies. Underestimation by the strip transect counts increased at high nest densities (Kendall  $t = -0.556$ ,  $P = 0.032$ ). The strip transect method needed on average 6.5 observers per colony surveyed, whereas the distance sampling method required 1.4 observers per colony. In addition, the mean time spent per colony was 3 hours vs 1.7 hours for the strip transect and distance sampling methods respectively. Combining both these measures of effort, distance sampling required on average 87% less effort in the field than the strip transect method. We strongly advocate the use of distance sampling for surveys of large gull colonies.

**RESUMEN.**—En este estudio comparamos dos métodos (conteo en transecto y muestreo por distancia) para estimar el número total de nidos en colonias de tres especies de gaviotas grandes. Se estudiaron 10 colonias utilizando ambos métodos. Las probabilidades de detección de nidos variaron entre  $0,519 \pm 0,064$  y  $0,706 \pm 0,049$ , y la probabilidad media de detección de un nido fue  $0,614 \pm 0,015$ . Las densidades de nidos fueron altamente variables, entre 77 y 717 nidos/ha. El número de nidos estimados mediante el método de transecto fue en promedio un 9,3% más bajo que el obtenido con el muestreo por

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distancia, aunque la diferencia alcanzó el 31% en algunas colonias. La discrepancia entre ambos métodos se incrementó con la densidad de nidos (Kendall  $t = -0,556$ ,  $P = 0,032$ ). El método de transecto necesitó en promedio 6,5 observaciones por colonia estudiada, en tanto que el de muestreo por distancia solo necesitó 1,4 observadores por colonia. Además, el tiempo medio pasado en cada colonia fue de 3 horas frente a 1,7 horas para el método por transecto y el de muestreo por distancia, respectivamente. Combinando ambas medidas de esfuerzo, el método de muestreo por distancia requirió en promedio un 87% menos de esfuerzo que el método de conteo en transecto. Proponemos firmemente el uso del método de muestreo por distancia en estudios de colonias de gaviotas grandes.

## INTRODUCTION

The monitoring of gull breeding colonies and populations is typically based on counts of active nests (Bibby *et al.*, 2000; Walsh *et al.*, 1995; Cadiou and Yésou, 2006). A frequently used method is the strip transect count, which consists of direct counts within entire colonies using transects. Typically the colony is divided into strips some two to three metres wide and observers zigzag across strips so as to cover all the area.

Counting gull colonies by the strip transect count method has several limitations. Firstly, several observers are often required to perform the counts, and time or the number of fieldworkers available may be limited. Secondly, observers may also vary in their experience and ability to detect nests. Thirdly, count duration may be significant in dense colonies, potentially increasing disturbance to breeding birds, and eventually affecting breeding parameters due to intra- and/or interspecific predation. Finally, this counting method often makes the *a priori* assumption that all nests are detected and counted. Therefore, the likelihood of finding a nest, i.e. nest detection probability, is not estimated. This assumption can bias the abundance and population trend estimates of programmes monitoring gull populations and, potentially, their conservation status and priorities (Barker and Sauer, 1992; Lancia *et al.*, 1994). Although gull nests may be highly detectable in some situations, there is clear evidence that the detection probability is not absolute

(Erwin, 1980; Ferns and Mudge, 1981; Wanless and Harris, 1984; Barbraud and Gélinaud, 2005).

Methods that take into account detection probability of objects during surveys, such as the double-observer or distance sampling methods, have been developed during recent decades (Thompson *et al.*, 1998; Buckland *et al.*, 2001; Williams *et al.*, 2002). However, the monitoring of gull breeding colonies is often undertaken using the strip transect or the sample quadrat count methods (Walsh *et al.*, 1995). The latter consists of counting nests in known-size quadrats disposed randomly or systematically in the colony. This allows estimating an average nest density which is then extrapolated to the entire surface of the colony. However, as for the strip transect method, the quadrat count method often assumes that all nests within quadrats are detected. Thus, there is a need for studies that compare the performance of these widely used methods with those that explicitly take detection probability into account (e.g. Robertson *et al.*, 2008).

Here, we use the distance sampling and the strip transect methods to estimate the number of active nests of herring gulls *Larus argentatus*, lesser black-backed gulls *Larus fuscus* and great black-backed gulls *Larus marinus* in Brittany (France) where some 65% of the French population of these three species breed annually (Cadiou *et al.*, 2004). Distance sampling has been used successfully in recent years to survey seabird nesting colonies (Lawton *et al.*, 2006; Kirkwood *et*

*al.*, 2007; Robertson *et al.*, 2008). Although few of these studies have compared the performances of different methods, Robertson *et al.* (2008) found that point distance sampling performed relatively well compared to other methods for surveying black-browed albatrosses *Thalassarche melanophrys* at Idelfonso (Chile). Similarly, Pyare *et al.* (2010) reported that distance sampling provided the most robust population estimate of Aleutian terns *Onychoprion aleutica* breeding in Alaska. The main advantages of the distance sampling method are that it is more efficient and causes less disturbance and that, unlike direct counts, it provides a confidence interval or error around the mean. In addition, distance sampling represents a statistically valid and repeatable method that can be applied during successive years. Contrary to the strip transect count method, observers are not constrained to a transect of a specific width and data collection is more efficient. Because the distance sampling method explicitly takes into account detection probability, and since it is unlikely that all nests in a given colony are detected, we predicted that the strip transect count method will underestimate the number of nests relative to the distance sampling method. The aims of this study were therefore to compare abundance estimates of active nests of large gull colonies obtained by both methods and the effort (number of fieldworkers and time spent in the field) required by both methods.

## MATERIAL AND METHODS

### *Study sites*

Fieldwork was carried out in Brittany, France, during the last two weeks of May 2009 and 2010, when a maximum number of nests have eggs in Brittany (Henry and Monnat, 1981). A total of 10 colonies were monitored; situated on the offshore islands of Belle-Ile (47° 20' N, 3° 10' W), Rohellan (47° 36' N, 3° 11'

W), Er Valant (47° 21' N, 2° 58' W), Er Valueg (47° 24' N, 3° 01' W), Meaban (47° 31' N, 2° 56' W), Er Lannig (47° 34' N, 2° 53' W) and Ile aux Oiseaux (47° 33' N, 2° 44' W). Colony sites were covered by herbaceous vegetation (mainly *Erica* spp., *Dactylis* spp., and *Ulex europaeus*) and rocky outcrops. Vegetation height was variable between colonies (10 cm to 1.5 m). All colonies but one were on flat areas and were occupied by at least one of the three surveyed species. Although nests of great black-backed gulls could be distinguished from nests of other species, nests of all species were pooled together in the analyses because nests of herring and lesser black-backed gulls cannot be easily distinguished in the field and great black-backed gulls were only nesting on three islands and sufficient numbers of their nests for a distance sampling analysis (> 50-60) were only available on two islands. The counting unit was the active nest: a fully constructed nest containing eggs and/or chicks, or an empty but well constructed nest judged capable of holding a clutch.

### *Strip transect counts*

Colonies were divided into parallel strips. At the beginning of each strip, observers (from 3 to 15) were aligned (one per strip) and separated by approximately 2 m. Observers covered the strips counting every active nest and noting the contents. Observers were asked to stay aligned and keep a constant inter-observer distance as much as they could. Each active nest found was marked with a small piece of paper safely disposed within the nest to avoid being removed by the wind. This ensured that nests were not counted twice. At the end of the count the total number of nests was the sum of the nests counted by each observer in the colony. For each colony, all strip transect counts were performed on precisely the same dates as the distance sampling line-transects.

### *Distance sampling*

Nest densities and their variances were estimated by line-transects using distance sampling (Buckland *et al.*, 2001). This method uses the perpendicular distance from the line to the object to correct for visibility bias, and allows estimating the probability of detecting objects and corrected densities. In each colony surveyed line-transects were distributed parallel and 20-50 m apart. Each transect line was covered by a single observer and the horizontal perpendicular distance from the transect line to each nest detected from the line was measured to the nearest 10 cm with a graduated pole. Nests to either side of the line were recorded. Line-transects were established using a hand-held GPS unit (Garmin 76CS). The observer walked in straight lines using the GPS unit navigation options. Densities were computed using Distance 5.0 software (Thomas *et al.*, 2010). For each line-transect, the truncation level was set following identification of outliers from box plots: outliers were values higher than 1.5 box-lengths from the 75<sup>th</sup> percentile. Truncation allows the detection of outliers that make modelling the detection function difficult (Buckland *et al.*, 2001). The probability of nest detection was estimated with models combining density functions (uniform, half-normal, and hazard-rate) with adjustments (cosine, simple, Hermite polynomials). The model with the lowest Akaike's Information Criterion value was selected for each colony (Burnham & Anderson, 2002). The adequacy of the selected model to the perpendicular distances was assessed by a chi-square goodness-of-fit test on grouped data and by verifying that coefficient of variation of the detection probability did not exceed 20% (Buckland *et al.*, 2001). Since goodness-of-fit tests are very sensitive to heaping we assessed heaping from histograms, and data were grouped where necessary (Buckland *et al.*, 2001). The four key assumptions of distance sampling are that: 1) objects on the line are detected with certainty ( $g(0) = 1$ ), 2) objects are detected at their initial

location, 3) measurements are exact, and 4) detections are independent events. To evaluate the first assumption, a sample of 10 transects randomly chosen among two colonies were covered by pairs of observers walking one behind the other. The first observer detected the nests from the line-transect and indicating all the detected nests to the second observer. The second observer systematically recorded whether some nests present within 10 cm of the line were missed by the first observer. No additional nest was detected by the second observer, so we considered  $g(0) = 1$ . Since nests were by definition immobile assumption two was satisfied. Given that distances were measured at  $\pm 10$  cm and that nests were found up to 15 metres from the line-transects we considered assumption three fulfilled. To satisfy the fourth assumption, when distances were measured, additional nests detected while walking from the line to the nests initially detected, but not detected from the line, were not included in the analysis. Numbers of nests were calculated by multiplying colony areas by mean densities estimated in the surveyed colonies.

Colony areas were calculated from aerial photographs and open source gvSIG 1.1.2 (<http://www.gvsig.com/>). During field surveys each colony was precisely mapped on an orthophotoplan derived from aerial photographs. The surface area of each colony was then determined using gvSIG.

Because the distance sampling method took into account the nest detection probability we predicted that the strip transect count method underestimated the number of nests. We thus evaluated the bias and accuracy of the strip transect count method for each colony.

### *Comparing methods and estimators*

To compare estimates of nest abundance obtained with the two methods we used three performance measures (Walther and Moore,

TABLE 1

Descriptors of the transect surveys at 13 gull colonies using the distance sampling method.

[Información sobre los muestreos en transectos en 13 colonias de gaviotas utilizando el método de muestreo por distancia.]

Colony	Date	Surface (m <sup>2</sup> )	Number of transects	Mean transect length (SD)	Number of nests found
Bordelan	15/05/2010	113009	10	229.0 (98.1)	154
Er Hastellic	14/05/2010	256853	10	675.7 (275.6)	286
Er Lannig	14/05/2009	7839	8	76.9 (22.4)	39
Er Valant	14/05/2009	31804	11	121.8 (41.6)	77
Er Valueg	14/05/2009	23237	9	93.7 (30.8)	106
Ile aux Oiseaux	29/05/2009	4680	10	46.8 (8.8)	109
Koh Kastell	13/05/2010	122384	21	144.3 (59.7)	339
Meaban	22/05/2010	17720	17	60.0 (30.6)	175
Talus	14/05/2010	39836	6	272.2 (95.1)	78
Vazen	13/05/2010	25776	9	177.9 (34.4)	66

2005). Bias was estimated as  $(N_{DS} - N_{Comp}) / N_{DS}$  where  $N_{DS}$  and  $N_{Comp}$  are respectively the number of nests estimated using the distance sampling and strip count methods. Accuracy was estimated as  $((N_{DS} - N_{Comp}) / N_{DS})^2$ . These metrics were scaled to allow comparisons between different colonies and values are provided for each colony separately. As another measure of accuracy we also estimated the percentage of estimates falling within the 5% range of  $N_{DS}$ . The lower and upper 5% range of  $N_{DS}$  was calculated as  $N_{DS} - N_{DS} / 20$  and  $N_{DS} + N_{DS} / 20$ , respectively. For each method we recorded simultaneously the number of observers involved and time spent during each colony count.

## RESULTS

Among the 10 colonies surveyed using both methods (table 1), colony surface area ranged from about 0.47-25.69 ha (mean 6.43 ha).

Within these colonies nest densities varied from 77-717 nests.ha<sup>-1</sup> (table 2). Nest detection probabilities were clearly lower than one, even within relatively narrow bands alongside transects (fig. 1). For example, the probability of detecting a nest within a 1.65 m band width was  $0.552 \pm 0.08$  (SE) at the Er Lannig colony (table 2).

Measures of bias and accuracy are shown in table 3 and figure 2. For all colonies except one, the strip transect count method underestimated the number of nests compared to the distance sampling method. This bias averaged -9.3% but reached -31% in some colonies. Mean square error accuracy of the strip transect count method was generally low ( $> 0.01$ , table 3). Bias was not significantly correlated with colony area (Kendall  $\tau = 0.022$ ,  $P = 1.0$ ) or the number of nests in the colony ( $\tau = -0.422$ ,  $P = 0.107$ ) but was significantly correlated with nest density ( $\tau = -0.556$ ,  $P = 0.032$ ). The underestimation of the number of nests obtained with the strip transect method

TABLE 2

Selected best models used for estimating nest densities for each gull colony. U, uniform distribution; HN, half-normal distribution; Truncation, right truncation distance in metres; GOF, goodness-of-fit P-value;  $\hat{D}$ , number of nests/ha;  $\hat{p}$ , nest detection probability; se, standard error. Right truncation consisted in excluding from the analyses nests situated at distances larger than 1.5 the 75<sup>th</sup> percentile of the distribution of the nest distances for each colony. Nest detection probability is the probability that an observer detects a nest situated between the line transect and the truncation distance.

[Selección de los mejores modelos empleados en la estimación de densidades de nidos para cada colonia de gaviotas. U, distribución uniforme; HN, distribución seminormal; Truncamiento, distancia de truncamiento a la derecha expresada en metros; GOF, significación de la bondad de ajuste;  $\hat{D}$ , número de nidos/ha;  $\hat{p}$ , probabilidad de detección del nido; se, error estándar. El truncamiento a la derecha consistió en excluir del análisis los nidos situados a una distancia 1,5 veces mayor al percentil 75 de la distribución de distancias de los nidos para cada colonia. La probabilidad de detección de los nidos es la probabilidad de que un observador detecte un nido situado entre la línea de transecto y la distancia de truncamiento.]

Colony	Model	Adjustment	Truncation	GOF	$\hat{D}$	se ( $\hat{D}$ )	$\hat{p}$	se ( $\hat{p}$ )
Bordelan	U	Cosinus	3.30	0.510	144.73	30.03	0.640	0.043
Er Hastelic	HN	All	3.20	0.917	92.46	13.36	0.648	0.037
Er Lannig	HN	Simple/Hermite	1.65	0.163	312.17	69.53	0.552	0.080
Er Valant	U	Simple	4.80	0.573	77.31	10.23	0.645	0.036
Er Valueg	U	Cosinus	3.45	0.237	244.53	36.29	0.689	0.063
Ile aux Oiseaux	U	All	2.25	0.403	717.83	117.26	0.519	0.064
KohKastell	HN	Cosinus	4.50	0.835	182.57	26.81	0.552	0.046
Meaban	U	Cosinus	2.85	0.472	440.85	88.13	0.581	0.031
Talus	U	Simple/Hermite	3.75	0.858	80.92	20.82	0.706	0.049
Vazen	U	Cosinus	4.50	0.335	76.45	20.10	0.590	0.052

compared to the distance sampling method was higher in colonies with the highest nest densities. Accuracy was not correlated with colony area, density or number of nests ( $P$ 's > 0.6). Only one (out of seven) nest counts estimated using the strip transect count method was included in the 5% range of distance sampling estimators.

The strip transect count method necessitated on average 6.5 observers per colony surveyed, whereas the distance sampling method only necessitated 1.4 observers per colony (table 4). In addition the mean time spent per colony was 3 vs 1.7 hours for the strip transect count and distance sampling methods respectively.

Combining both measures of effort (number of observers per colony multiplied by time spent per colony), the distance sampling method required on average 87.5% less effort in the field than the strip transect count method. This was very consistent between colonies as indicated by the low standard deviation of the average estimate (4.2%).

## DISCUSSION

As expected, the strip transect count method, which does not take detection probability into account, underestimated the number

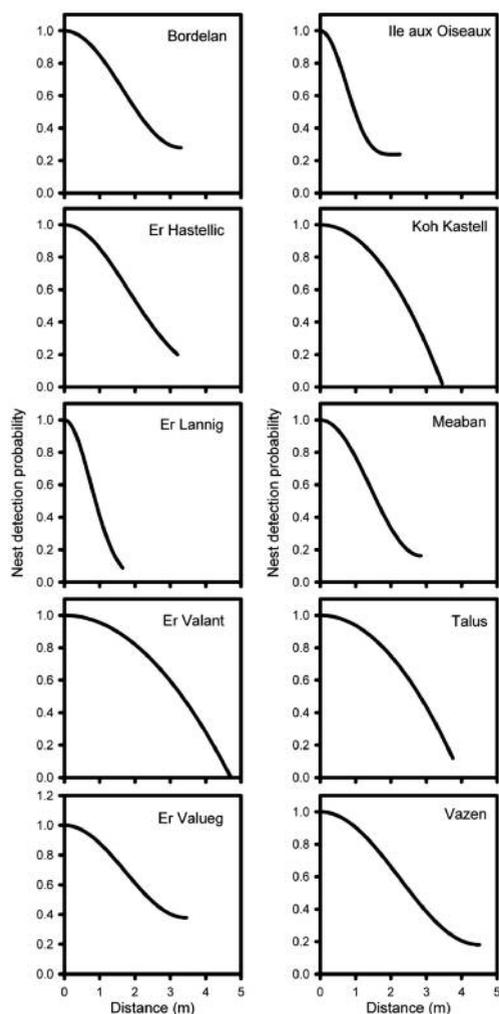


FIG. 1.—Detection probability functions for each colony as modelled in table 2. Truncation distance varies according to colony (table 2).

[Funciones de la probabilidad de detección de un nido en cada colonia de acuerdo a los modelos en la tabla 2. La distancia de truncamiento varía dependiendo de la colonia (tabla 2).]

of occupied nests in breeding colonies of large gulls when compared with the distance sampling method. Bias averaged around  $-9\%$  but varied between c.  $12\%$  and c.  $-31\%$ . This

suggests that considerable underestimation may occur using the strip transect count method, which can potentially have important consequences for inferences on population status and trends. We found significant variations in bias and accuracy between colonies. With respect to bias, our results suggest that this was partly due to variation in nest density. In colonies where nest density was high ( $> 200$  nests.ha $^{-1}$ ), the strip transect method underestimated the number of nests by  $> 10\%$  compared to the distance sampling method, whereas bias was lower at low nest densities. Thus, observers using the strip transect method were probably more likely to miss nests in colonies with high nest densities. However, other factors such as differences in observer experience may also have played a role (e.g., Barbraud and Gélinaud, 2005), although they were not quantified and modelled here. Nevertheless, regardless of the causes of the bias, we recommend the use of a method that explicitly accounts for nest detectability, such as the double observer method (Barbraud and Gélinaud, 2005) or the distance sampling method, when estimating the abundance of large ground-nesting gulls.

It can be stressed that the strip transect method covers an area in relatively narrow transects (usually 2-3 m wide) that are prospected in a zig-zag, and therefore the problem of a decrease in nest detection probability with distance is relatively minor. However, results from the distance sampling analysis showed that the average nest detection probability was well below 1 ( $\approx 0.61$  from table 2) at an average distance of  $\approx 3.4$  m, suggesting that a significant proportion of nests may not be detected during strip transects. Indeed, when the truncation distance was fixed at 2 m for all models showed in table 2, the average detection probability was 0.79 (min: 0.52, max: 1.00). In addition, nest detection probability varied significantly among colonies, which may partly explain the variation in bias observed between both methods. Although we did not record

TABLE 3

Estimates of the number of nests in gull colonies and performance measures. Estimates obtained using the distance sampling method are:  $\hat{D}$  the nest density in nest.ha<sup>-1</sup>,  $\hat{N}_{DS}$  the number of nests in the colony,  $L(\hat{N}_{DS})$  and  $U(\hat{N}_{DS})$  the lower and upper 95% confidence interval limits of  $\hat{N}_{DS}$ .  $N_{Comp}$  is the number of nests obtained using the strip transect count method. Range indicates whether the strip transect count falls within the range of the 95% confidence interval limits. Mean bias was  $-0.0933 \pm 0.1095$  (sd).

[Estimas del número de nidos en colonias de gaviotas y medidas de desempeño. Las estimas obtenidas utilizando el método de muestreo por distancia son:  $\hat{D}$  densidad de nidos en nidos/ha;  $\hat{N}_{DS}$  número de nidos en la colonia,  $L(\hat{N}_{DS})$  y  $U(\hat{N}_{DS})$  límites inferior y superior, respectivamente, del intervalo de confianza de  $\hat{N}_{DS}$ .  $N_{Comp}$  es el número de nidos obtenido utilizando el método de conteo de transecto en banda. El rango (Range) indica si el conteo de transecto en banda cae dentro del rango de los límites de los intervalos de confianza al 95%. El error en la media fue  $-0.0933 \pm 0.1095$  (sd).]

Colony	$\hat{N}_{DS}$	$L(\hat{N}_{DS}) - U(\hat{N}_{DS})$	$N_{Comp}$	Bias	Range
Bordelan	1636	1042 – 2567	1471	-0.1009	No
Er Hastellic	2375	1739 – 3243	1984	-0.1646	No
Er Lannig	245	153 – 391	220	-0.1020	No
Er Valant	246	140 – 431	238	-0.0325	Yes
Er Valueg	568	418 – 773	390	-0.3134	No
Ile aux Oiseaux	336	243 – 464	300	-0.1071	No
Koh Kastell	2234	1667 – 2995	2065	-0.0756	No
Meaban	781	516 – 1183	697	-0.1076	No
Talus	322	173 – 602	304	-0.0559	No
Vazen	197	111 – 350	222	0.1269	No

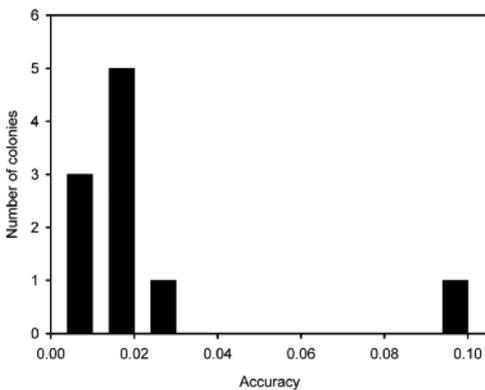


FIG. 2. — Frequency distribution of the accuracy calculated for each colony.

[Distribución de frecuencias de la precisión estimada para cada colonia.]

habitat covariates or nest visibility covariates, the two colonies with the lowest nest detection probability (Ile aux Oiseaux and Er Lannig) were those where vegetation cover was the highest (1-1.5 m) compared to other colonies (usually from 0.5-1 m).

In addition to biased estimates, the strip transect method required a much greater effort in the field compared to the distance sampling method: on average c. 4.6 times more observers were needed and the time spent in colonies was on average c. 42% longer than with the distance sampling method. For optimal use of resources, and since the number of available observers is often limited when conducting surveys of gull colonies, we strongly recommend using the

TABLE 4

Allocation of effort for the strip transect and distance sampling methods during surveys of colonies of large gulls in Brittany, France.  $n_{\text{obs}}$  is the number of observers and *time* the time needed to survey the entire colony.

[Asignación del esfuerzo realizado utilizando los métodos de conteo en transecto y de muestreo por distancia durante estudios de colonias de gaviotas grandes en Bretaña, Francia.  $n_{\text{obs}}$  es el número de observadores y *time* el tiempo necesitado para muestrear toda la colonia.]

Colony	Strip transect		Distance sampling		Difference $n_{\text{obs}}$ (%)	Difference time (%)
	$n_{\text{obs}}$	time (h)	$n_{\text{obs}}$	time (h)		
Bordelan	5	4	2	2.0	-60.0	-50.0
Er Hastellic	9	4.5	2	2.0	-77.8	-55.6
Er Lannig	5	1.5	1	1	-80.0	-33.3
Er Valant	6	3	2	1.5	-66.7	-50.0
Er Valueg	6	3	2	1.5	-66.7	-50.0
Ile aux Oiseaux	5	1.5	1	1	-80.0	-33.3
Koh Kastell	9	4.5	1	3.5	-88.9	-22.2
Meaban	8	3	1	1.5	-87.5	-50.0
Talus	6	3	1	1.5	-83.3	-50.0
Vazen	6	2	1	1.5	-83.3	-25.0
<i>Mean</i>	6.5	3.0	1.4	1.7	-77.4	-41.9
<i>(SD)</i>	(1.6)	(1.1)	(0.5)	(0.7)	(9.7)	(12.2)

distance sampling method for such surveys. In addition, this would considerably limit the disturbance within the colony during the counts, since fewer observers are needed and less time is spent, thereby minimising intra- and/or interspecific nest predation. A simplistic distance sampling method approach such as that presented here could even be desirable to reduce effort and disturbance, particularly when dealing with sensitive species, even at the expense of larger potential biases. Compared to the double-observer method (Nichols *et al.*, 2000; Barbraud and Gélinaud, 2005) or capture-recapture methods (Nichols *et al.*, 1986), the distance sampling method will often only require a single observer, whereas at least two are needed for the other methods and repeated count sessions are required when

using capture-recapture. Regarding disturbance, the distance sampling approach requires measurements with high precision which potentially takes time to be conducted. Therefore in dense colonies or at specific areas of a colony disturbance by distance sampling and strip transect sampling may be relatively similar. From our experience of the colonies surveyed, distance measurements are rapidly performed in the field with an appropriate tool such as a pole with marks every 10 cm or using a laser rangefinder for distances > 5 m. We are thus convinced that the main assumptions of the distance sampling method will most often be fulfilled when surveying gull nests in colonies. If observers suspect that some nests are missed on the transect line [i.e. and in this case  $g(0) < 1$ ], then a mark-recapture distance

sampling method may be useful (Borchers *et al.*, 1998).

Although we obtained pooled estimates of the number of nests for all three species, separate estimates for greater black-backed gulls and herring/lesser black-backed gulls could be obtained using the distance sampling method. The eggs, nest structure and nest shape of herring and lesser black-back gulls are extremely difficult to distinguish irrespective of the sampling method used. However, assuming identical detection probability, a ratio of nests of greater black-back gulls to total number of nests in colonies where greater black-backed gulls breed can be calculated and incorporated in the distance sampling analysis to obtain an estimate of the number of nests of greater black-backed gulls for those colonies. Alternatively, if differences in nest detection probability are suspected between nests of greater black-backed gulls and herring/lesser black-backed gulls, and if sufficiently large samples can be obtained, separate distance sampling analyses can be performed to estimate species-specific numbers of nests.

However, the distance sampling method is also subject to potential biases arising from habitat or density heterogeneity. Gull colonies may be heterogeneous in habitat, which can result in density heterogeneity. Habitat heterogeneity was not taken into account in our study (a single detection function was fitted for each colony) since within colonies habitat was relatively homogeneous. Thus, although the distance between transects varied between 20 and 50 m (due to logistical constraints) and our detection range was below 10 m, habitat heterogeneity is unlikely to have affected our results. Nevertheless, we cannot exclude that better estimates could have been obtained by stratifying our sampling as a function of nest density, by fitting different detection functions for the core and edge areas of the colonies. Thus, in colonies where habitat is highly heterogeneous the sampling can be stratified by habitat classes and specific detection functions can be fitted to each class, provided sufficiently

large sample sizes can be obtained for each class. Ideally, the ratio length of transects / area of the colony and separation between line transects should be kept relatively constant to homogenize sampling effort among colonies.

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