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Comparison of Distance Sampling and Territory Mapping

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**Comparison of Distance Sampling and Territory Mapping methods for
birds in four different habitats**

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1 **Abstract**

2 Distance sampling (DS) and territory mapping (TM) are globally applied bird survey
3 techniques. However, specifically designed studies comparing results of both methods in
4 different habitats in the framework of a scientific experiment have rarely been conducted. To
5 provide a more generalized guidance for the field surveyor, here we evaluated estimates of
6 bird abundances and number of bird species in four different habitats (broad-leaved forest,
7 coniferous forest, open woodland and farmland) in central Germany. Abundances were
8 estimated in parallel by TM and DS in 2006 and 2008, following standard protocols.
9 Detection probability differed significantly among habitats and species. Density estimates by
10 DS were in total 24% lower than those estimated by standardized TM. While the number of
11 bird species detected with both methods was approximately the same, the estimated
12 abundances of 15 bird species showed significant differences. Increasing the number from
13 two to four and five registrations to count a territory by using TM decreased the density on
14 average about 28% and 42%, respectively. Using standardized TM resulted in an
15 overestimation of abundances of species showing a high detection probability. In contrast, DS
16 estimated very high densities for species that had a very low detection probability. In fact, a
17 highly negative correlation was found between the density estimated by DS and the detection
18 probability. Using standardized TM and setting a fixed number of registrations before a
19 location qualifies for a bird territory cannot compensate for the large differences in species
20 detectability. Instead, the number of registrations required to count a territory should be
21 adjusted to differences in detection probabilities and seasonal activity. From our results we
22 can recommend a mean of four registrations if eight visits were conducted to count a territory.
23 However, the lack of any statistically-based quality assessment reduces the serious usability
24 of TM for estimating densities for science-based management applications. Whereas, the clear
25 advantage of DS is that it provides error estimates and considers differences in species
26 detectability.

27 *Key words:* bird census, detection probability, number of registrations, habitat type, survey
28 design

29

30 **Zusammenfassung**

31 **Ein Vergleich zwischen Distance Sampling und Revierkartierung zur Erfassung von** 32 **Vogelbeständen in vier verschiedenen Lebensräumen**

33 Distance Sampling (DS) und Revierkartierung gehören zu den verbreitetsten
34 Erfassungsmethoden von Vogelbeständen weltweit. Bisher gibt es kaum Studien bei denen im
35 Rahmen eines wissenschaftlichen Experiments beide Methoden parallel durchgeführt und die
36 Ergebnisse verglichen wurden. Ziel der im Jahr 2006 und 2008 im Hohen Vogelsberg, Hessen
37 durchgeführten Untersuchung war es deshalb, jeweils die Artenanzahl und die Abundanzen
38 von Vögeln sowohl mit DS als auch mit der Revierkartierung in vier unterschiedlichen
39 Lebensräumen (Laubwald, Nadelwald, Halboffenland und Offenland) standardisiert zu
40 erfassen und zu vergleichen. Die Erfassungswahrscheinlichkeit unterschied sich deutlich
41 zwischen den Lebensräumen und zwischen den Vogelarten. Die Dichten, die mit Hilfe von
42 DS erfasst wurden, fielen im Durchschnitt um 24% niedriger aus im Vergleich zu den mit der
43 Revierkartierung ermittelten Dichten. Während die Anzahl der ermittelten Arten bei beiden
44 Methoden in etwa gleich war, zeigten die Abundanzen von 15 Arten signifikante
45 Unterschiede. Bei der standardisierten Revierkartierung wurde ein Revier nur dann gezählt,
46 wenn mindestens zwei Registrierungen der Art erfolgten. Steigert man die Anzahl der
47 notwendigen Mindestregistrierungen auf vier bzw. fünf reduzierte sich die Dichte im
48 Durchschnitt um 28% bzw. 42%. Die standardisierte Revierkartierung führte zu einer
49 Überschätzung der Bestände von Vogelarten mit einer hohen Erfassungswahrscheinlichkeit.
50 Im Gegensatz hierzu wurden mit DS sehr hohe Dichten für Arten mit geringer
51 Erfassungswahrscheinlichkeit ermittelt. Dies verdeutlicht die festgestellte negative
52 Korrelation zwischen Dichte und Erfassungswahrscheinlichkeit. Die Verwendung der

53 Revierkartierung mit einer fixen Anzahl von Mindestregistrierungen zur Zählung eines
54 Reviers wird den unterschiedlichen Erfassungswahrscheinlichkeiten zwischen den
55 verschiedenen Vogelarten nicht gerecht. Daher empfiehlt sich ein artspezifisches Vorgehen
56 unter Berücksichtigung der Erfassungswahrscheinlichkeit und der saisonalen Aktivität.
57 Unsere Ergebnisse zeigen, dass zur Wertung eines Reviers im Durchschnitt vier
58 Registrierungen eines Vogels bei acht Begehungen notwendig sind, um realistischere
59 Abundanzen zu erhalten. Das Fehlen jeglicher statistischer Angaben zur Bestimmung der
60 Erfassungsgüte bei der Revierkartierung reduziert deren Eignung, um wissenschaftlich
61 fundierte Aussagen zu erhalten. DS bietet dagegen den großen Vorteil, dass es zu jeder
62 berechneten Abundanz Konfidenzintervalle und den jeweiligen Fehler liefert.

63

64

65 Distance sampling (DS) and territory mapping (TM, or spot-mapping) are survey techniques
66 for estimating bird abundance (Bibby et al. 2000, Buckland et al. 2001). The TM method is
67 based on counting territories of all species within a defined study plot. Locations of all birds,
68 particularly singing males, are mapped on paper replicas of the plot during visits (usually
69 eight or more) during the breeding season. Data for each visit are transcribed to species-
70 specific sheets, and territory boundaries are identified for clustered multiple registrations at
71 the end of the census.

72 The DS method is based on counting birds detected as heard or seen from a point or
73 transect (Buckland et al. 2001), and takes into account the fact that some birds are detectable
74 at greater distances than others, that a species may be more easily detected in one habitat than
75 another, and that detectability can change with time of day. Therefore, for each bird detected,
76 the distance between observer and bird must be estimated accurately. A detection function is
77 estimated from these distance data, and is then used to compute the probability of detection.
78 Crucial to DS is the estimated detection function that compensates for the fact that
79 detectability decreases with increasing distance from the observer. Studies have shown that
80 DS delivers reliable results and is efficient for sampling large areas (Norvell et al. 2003,
81 Somershoe et al. 2006, Newson et al. 2008, Ronconi and Burger 2009). To create detection
82 functions for each bird species, a minimum number of observations in each main habitat is
83 required. Alternatively, detection probability functions of biologically similar species can
84 sometimes be used (Buckland et al. 2008). However, the assumption of a similar, constant and
85 transferable detection probability can be difficult, especially for rare species and when survey
86 conditions vary. Experience shows that detection is highly dynamic and can vary with time of
87 day, between seasons, years and other factors (Norvell et al. 2003, Robbins 1981).

88 TM attempts to account for imperfect detection by using a fixed ratio of registrations
89 of a species to the number of effective visits for that species. This ratio, usually similar for all

90 species, is used to decide whether a territory will be assigned for counting. Bibby et al. (2000)
91 recommended at least two registrations for a species if there were eight or fewer visits, and at
92 least three registrations when there are nine or more visits. This rule corresponds to a fixed
93 detection rate of around 0.25-0.33. Despite the inability to assess this rule or its validity in a
94 scientific way, using a constant number in that range will result in uncertainties if used for
95 estimating abundances for a whole study area. Furthermore, territories of birds can be highly
96 dynamic within the season (Knapton and Krebs 1974, Finck 1990, Pasinelli 2000), making the
97 territory a questionable metric for abundance estimation. One assumed strength of TM is that
98 it provides finer spatial detail and, therefore, can be better used to depict the spatial
99 distribution pattern of birds in an area and, additionally, can be correlated with habitat
100 distribution. Therefore, it is often applied in environmental assessment studies because areas
101 important to birds can be identified.

102 Despite the popularity of both methods, few investigators have compared the actual
103 results of bird abundance estimation using DS and TM in the same study area. Such studies
104 are very helpful for assessing and interpreting the accuracy and possible biases of each
105 method. To our knowledge, the only studies where birds were estimated by both DS and TM
106 by using a standardized approach and the two methods compared were those of Gillings et al.
107 (1998), Raman (2003) and Buckland (2006). The results of these studies did not show a clear
108 pattern, Buckland (2006) and Gillings et al. (1998) estimated for three species a lower, for
109 three other species a higher and for two species a similar density using TM compared to DS.
110 Raman (2003) estimated a higher density using TM compared to DS for two out of 13 species
111 in a tropical rainforest. Although Bibby et al. (2000) has shown that territory maps are not
112 easy to analyze and can be interpreted differently, depending for instance on the number of
113 registrations used to set a territory (Gerß 1984), none of these studies reported how territories
114 were detected, and with the exception of Gillings et al. (1998) the minimum number of
115 registrations used to set a territory was not reported. None of the studies comparing DS and

116 TM analyzed the influence of the minimum number of registrations on the estimated
117 densities. However, this number is important as it indirectly reports the assumed detection
118 rate, which is crucial to reduce over- or underestimation of species density. Further, detection
119 rates differ between habitats (Buckland et al. 2001, Pacifici et al. 2008) but none of the
120 previous studies have compared the densities estimated in different habitats and using both,
121 TM and DS. Therefore, we used a standardized sampling design and conducted a field study
122 in four different habitats which were selected for their differences in vegetation structure (Fig
123 1). Our objective was to provide guidance to the field surveyor. Therefore, we determined if
124 (1) the strength of differences between the results of both methods are habitat specific, (2) the
125 number of registrations used to set a territory influence densities estimated by TM and (3) the
126 differences in species detectability affect estimates of species densities by TM and DS,
127 respectively. To do so, abundances and number of bird species were estimated by both
128 methods.

129 We decided not to set one method as a benchmark *a priori* (e.g. Buckland 2006,
130 DeSante 1986, Gale et al. 2009), as we do not assume that one of the methods provides
131 greater precision *per se*. Further, intensive bird census techniques used in other studies
132 (Casagrande and Beissinger 1997, DeSante 1986, Tarvin et al. 1998) like color-banding or
133 nest-finding do not guarantee that individuals can be found or caught with equal ease and it is
134 very difficult to be confident that all individuals have been found (Bibby et al. 2000).
135 Additionally, these techniques are likely to result in an unacceptable level of disturbance to
136 birds.

137

138 **Methods**

139 All study sites were located in the Hoherodskopf, located 60 km northeast of Frankfurt
140 am Main in Hessen, central Germany (9°21'E and 50°51'N). One study site was located in
141 each of four habitats: beech forest (*Fagus sylvatica*), coniferous forest, open woodland, and

142 farmland. Study sites where TM got conducted were limited to 25 ha to avoid census times
143 exceeding the morning peak of bird activity. To reduce possible edge effects, the shapes of
144 the study sites were chosen for compactness.

145 The beech forest study site was located on the north-eastern slope of the Hoherodskopf
146 (710-760 m) and consisted mainly (86%) of 50-year-old beech trees. Small patches of older
147 beech trees were present, along with maple trees (*Acer pseudoplatanus* and *A. platanoides*)
148 and common spruce (*Picea abies*). The coniferous forest was located in the southern slope of
149 the Hoherodskopf (630-675 m); most (95%) of the area was covered by spruce, with small
150 openings of grassland. The open woodland was located on the north-western slope of the
151 Hoherodskopf (660-725 m) and consisted of European mountain ash (*Sorbus aucuparia*) and
152 white willow (*Salix alba*), grassland and patches of myrtle blueberry (*Vaccinium myrtillus*) on
153 open areas. The farmland was located on a northwest slope (480-535 m), and consisted of
154 approximately 55% grassland and 40% barley (*Hordeum vulgare*) crops. Additionally, single
155 trees, hedges, and grassland field boundaries were present.

156 **Counting methods.** We visited beech forest, open woodland, and farmland eight
157 times between 29th March and 17th July 2006 and the coniferous forest between 4th April and
158 25th June 2008. Survey work was repeated a minimum of one week after the previous visit.
159 Six of eight surveys started 30 min before sunrise and finished between 08:00 and 11:00
160 (mean = 09:37). Two of the eight visits were in the evening to better sample species less
161 active in the early morning, e.g., raptors and owls. All surveys were conducted by the same
162 observer. To obtain comparable conditions and data, DS and TM were conducted on the same
163 day; the second method was started after the first was completed. The order in which each
164 method was used first was alternated. Before the field work was started, a route was
165 established on a map that approached within 50 m of every point on the plot. In open
166 woodland and farmland, where visibility was higher, this distance was set to a maximum of
167 100 m. Although we are aware that the first day survey (TM or DS) could influence both, the

168 observer (because of a priori knowledge from the first survey) and the birds (because of
169 disturbances by the first survey), during the second survey of this day we considered these
170 points with possible day-to-day differences in weather conditions (Bibby et al. 2000) if the
171 census would have been conducted on two different days and differences in observers
172 perception (Diefenbach et al. 2003) if the census would have been conducted from two or
173 more observers.

174 Following Bibby et al. (2000) for TM, the locations of all birds present in the plot
175 were mapped on different days, and a territory was defined if at least two registrations were
176 made of a bird singing or exhibiting breeding behavior (nest with eggs, young birds, or adults
177 carrying nest material or food). Henceforth, we call this the ‘standardized TM’ approach. To
178 analyze the effect of the minimum number of registrations used to count a territory, the
179 number of registrations used to set a territory was increased from two to five. Assuming that
180 each territory was occupied by a pair, the number of territories was equivalent to the number
181 of breeding pairs in the plot.

182 DS was conducted using point counts where all birds heard or exhibiting breeding
183 behavior within 5 min were mapped. We decided to use 5 min instead of 10 min as it reduces
184 the chance of double counts and is widely used. Distance to each bird detected was estimated
185 to the nearest 10 m-interval using binoculars (8 x 56) that included a laser range finder.
186 Sampling points were placed within the study sites where TM was conducted, and spaced at
187 least 200 m apart to reduce spatial autocorrelation. Without overlap, six sampling points could
188 be placed within each 25-ha study plot. All were marked for easy relocation on later visits.

189 All point-count data were analyzed using the program DISTANCE (version 5.0,
190 Thomas et al. 2009). We truncated point-count distances at 150 m. Therefore, an area of 42.4
191 ha in each habitat was analyzed. Detections for all visits were pooled for each of the four
192 study sites. The survey effort parameter was set to eight based on the number of visits to each
193 site. However, following Südbeck et al. (2005), the survey effort parameter was set to seven

194 for two migrant species (Tree Pipits, *Anthus trivialis*, and Eurasian Blackcaps, *Sylvia*
195 *atricapilla*) and, for Common Whitethroats (*Sylvia communis*), to six due to their later arrival
196 on their breeding grounds. Abundance estimates of species showing a coefficient of variation
197 (CV) higher than 40% were not analyzed. In our study, at least 20 registrations were needed
198 for the CV to fall below this value. We did not pool data across habitats to facilitate
199 comparisons of detection probabilities across individual habitats. An average of 66 detections
200 per species of singing birds was used to analyze bird data with DISTANCE. For some
201 species, the number of detections was lower than the 60 recommended by Buckland et al.
202 (2001), but reliable detection curves could still be fitted. According to the methodology and
203 definition of both census methods used, the output of TM are territories and that of DS are
204 birds. However, in fact in both methods singing birds, or birds showing clues of breeding
205 behavior, were counted.

206 To examine how density is related to detectability, correlations between abundance
207 values and the effective detection radius (EDR) were analyzed using Spearman rank order
208 correlations. EDR represents the distance from the observer where the number of birds missed
209 equals the number of birds observed farther away (Gates 1979). EDR and its coefficient of
210 variation for each species were calculated using the program DISTANCE. Densities
211 determined for the two methods were compared using the Wilcoxon matched pairs test. To
212 identify possible differences in detection probability among habitats, we used one-way
213 ANOVA. All statistical analyses were conducted using the Statistica 7.1 software package
214 (StatSoft Inc., Tulsa, OK).

215

216 **Results**

217 We detected 58 species with DS and 60 with TM. The small differences in number of
218 species detected were caused by the varying number of non-breeding birds (overflying birds
219 or migrants). Eight and six of these non-breeding species were found using TM and DS,

220 respectively. Most bird species were found in half-open woodland (39 species using DS and
221 38 using TM) and farmland (31 species using DS and 39 using TM) and lowest species
222 diversity was observed in beech and coniferous forest (30 and 28 species using DS and 31 and
223 33 using TM, respectively). Thus, the number of bird species counted by DS and TM showed
224 the highest difference in farmland. This difference is mainly caused by a relatively higher
225 number of non-breeding birds species counted using TM (six species) than using DS (two
226 species). In other habitats the same number of bird species or none non-breeding birds were
227 recorded using TM and DS.

228 We calculated abundances for 15 of these species (species with CV below 40%) and
229 compared all together 22 density values from the four habitats (Table 1). Densities estimated
230 by DS were significantly lower (in total by 24%) than those estimated by the standardized TM
231 approach (Wilcoxon Matched Pair Test, $n=22$, $z = 2.68$, $p = 0.013$). Abundances estimated
232 from the standardized TM approach were up to 3.9 times higher (mean = 1.3) than those
233 derived from DS. Only Chaffinches in beech forest and Firecrests and Goldcrests in
234 coniferous forest showed significantly higher abundances using DS. The strength of
235 differences between the estimated densities varied between habitats. On average differences
236 increased by 1.0 territories / 10 ha in farmland, 2.0 territories / 10 ha in beech forest, 2.8
237 territories / 10 ha in open woodland and 5.5 territories / 10 ha in coniferous forest. Highest
238 differences with more than four territories / 10 ha were estimated solely for species found in
239 coniferous forest (Robin, Common Wood Pigeon, Common Chaffinch, Winter Wren,
240 Common Blackbird, Firecrest and Goldcrest).

241 Densities of all bird species decreased with an increasing number of registrations used
242 to count a territory. The mean density of the 15 bird species analyzed decreased about 34%
243 from 8.8 territories/10 ha using two registrations to 5.1 territories/10 ha using five
244 registrations. The number of registrations was negatively correlated with density ($r_s = -0.39$,
245 $p = 0.000229$) estimated by TM. Densities based on two and three registrations differed

246 significantly from those estimated by DS (Wilcoxon Matched Pair Test, $n=22$, $z = 2.68$,
247 $p = 0.013$ and $n=22$, $z = 2.19$, $p = 0.028$).

248 Detection probabilities differed among habitats (one-way ANOVA, $F_{3,19} = 3.6$,
249 $p = 0.032$) and species (Fig. 1). Lowest EDR was generally found in beech forest
250 (mean = 79 m, range = 71 - 110 m, $n = 7$) followed by coniferous forest (mean = 87 m, range
251 = 29 - 132 m, $n = 10$), farmland (mean = 100 m, range = 94 - 106 m, $n = 3$) and open
252 woodland (mean of 137 m, range = 124 - 150 m, $n = 3$). Detection probability decreased from
253 more loud and conspicuous species (e.g. Tree Pipit, EDR = 150 m and Common Chaffinch,
254 EDR = 138 m) to the more elusive species in the study plots (e.g. Goldcrest EDR = 34 m and
255 Firecrest EDR = 29 m) (Table 1). A negative correlation was identified between the density
256 estimated by DS and the detection probability (EDR) (Spearman Rank Correlation: -0.66,
257 $p = 0.000853$) (Fig. 2). All densities estimated by TM regardless the number of registrations
258 used to count a territory did not correlate with the EDR.

259 The time required to conduct the bird survey varied between habitat and survey
260 techniques (Table 2). Using TM, most time was spent in the coniferous forest, followed by
261 beech forest, farmland, and open woodland. DS was the more efficient method: almost twice
262 as much time was required to conduct the bird census using the TM method.

263

264 **Discussion**

265 We found that the number of species detected was similar using DS and TM.
266 Generally, the number of species detected was related mostly to habitat, the study area size
267 (TM: 25 ha and DS: 42.4 ha), survey effort (TM: 137min and DS: 70min at mean), and the
268 detection probability of each species (Fig. 1). Although the time spent on each study site was
269 higher using TM and would allow more opportunity to detect bird species, the area surveyed
270 using DS was larger and therefore potentially inhabited by a larger number of bird species.

271 The strength of difference between the estimated abundances of both methods was
272 related to habitat. Largest differences between both results were found in coniferous forest
273 and were lowest in farmland. This suggests that estimated densities from habitats like the
274 coniferous forest where bird species show a low EDR are more sensitive to methods which
275 take the detection probability into consideration.

276 One reason for the higher density estimates obtained in our study by the standardized
277 TM approach when compared to DS was the static number of registrations. For our
278 standardized TM approach, we followed Bibby et al. (2000) who recommended at least two
279 registrations if there were eight visits to the study area. This number essentially assumes a
280 detection probability of 25% for all bird species and thus ignores crucial and dynamic
281 differences in the detection probability between species. Densities estimated by TM based on
282 four and five registrations (detection probability of 50%-62.5%) were lower and did not
283 significantly differ from those estimated by DS. These results confirm the findings of Gerß
284 (1984) who has shown in an experiment using an automated approach to demarcate territories
285 that the number of territories is largely affected by the minimum number of observations used
286 to count a territory. The minimum number of territories used in TM also explains the
287 differences between our results and those of Gillings et al. (1998). They compared bird
288 density estimates using TM and DS in the UK, and conducted four visits and counted one
289 territory if at least two registrations were made using TM and 0.5 territories if one registration
290 was conducted. The chance to detect a bird during four visits was lower than in our study and
291 thus, fewer birds were registered by using TM. Consequently, these densities were more
292 similar to the lower densities estimated by DS. This example emphasizes that detected
293 differences have to be analysed exactly by how territories have been estimated using TM.
294 The reasons in our study for the differences found between the four densities estimated by
295 TM using a different minimum number of bird registrations are related to (a) edge clusters,
296 when territories overlap the plot boundary (Bibby et al. 2000), and (b) the assumed minimum

297 Euclidian distance at which an observation will be included to a territory (Scheffer 1987).
298 Following Dornbusch et al. (1968) we counted a territory as a half if more than 50% of the
299 observations of an edge cluster were inside the plot. Thus, and confirming the finding of Gerß
300 (1984), the reduction of the minimum number of registrations increases the chance that such a
301 territory can be counted in. The second reason is related to the minimum distance at which an
302 observation was assumed to belong to a territory. When increasing the minimum number of
303 registrations used to count a territory, an increasing number of registrations of greater distance
304 from each other are used to set the territory. To minimize those effects and to reduce observer
305 variation, which is common when TM results were analysed (Best 1975, Svensson 1974), an
306 automated territory clustering approach is helpful (Gerß 1984 and Scheffer 1987) especially
307 when combined with a GIS (Witham and Kimball 1996). Such an approach can help to
308 standardize and automate territory interpretation and to find the “correct” number of
309 territories. Therefore, it should incorporate species-specific standards, e.g. minimum number
310 of registrations to count a territory, maximum distance between registrations at which they
311 will be used to set a territory. However, these standards can not diminish drawbacks that arise
312 from ignoring differences between species detection probabilities. As shown in our study, the
313 detection probability differs between species. This suggests that using TM and simply setting
314 a fixed number of registrations for a species until it qualifies for a territory cannot compensate
315 for the huge differences in species detectability. It is not clear to us where this static number
316 of registrations used for TM has its primary and scientific origin, and what its underlying
317 logic, data and tests are. Compared to this static value, DS instead estimates empirically a
318 more realistic correction factor, based on the true survey circumstances of each actual
319 detection event (Buckland et al. 2001).

320 The unexpected significantly high negative correlation between detection probabilities
321 and densities estimated by DS suggests that DS may overestimate quiet or cryptic species,
322 especially if patchily distributed, relative to large and conspicuous species. This could be for

323 the reason that DS assumes a uniform distribution within one habitat for a given study area
324 (Buckland et al. 2001). If a high number of birds were counted at small distance, an
325 overestimation of the abundance of these species by DS might be possible, especially if
326 species occur in clusters or when density varies throughout the study area. To reduce the
327 influence of this biased information on the distribution, the pattern of habitat characteristics
328 can be used by modelling abundance covariate effects in DS models to reach reliable density
329 estimates (Marques et al. 2007, Royle et al. 2004). Furthermore, to control for variation in
330 detection probability, sampling points can be visited more frequently or placed at higher
331 densities within areas where quiet or cryptic species might occur and vegetation structure
332 varies (Buckland et al. 2004). The DS software is helpful for designing appropriate survey
333 strategies in such studies. In our study, significantly higher densities of Goldcrest and
334 Firecrest were estimated using DS compared to TM. The detection probability curves for
335 these species showed steeply declining curves and low effective detection radii. According to
336 these curves, a detection probability of 0.5 for Goldcrest and Firecrest can be reached at a
337 distance of 29 m and 34 m, respectively. In practical terms, this means that every second
338 individual would not be detected at these distances. As recommended in Bibby et al. (2000),
339 TM was conducted by an observer walking lines 50 m apart; resulting in a 21 m and 16 m
340 survey gap respectively. However, to detect more individuals of species having a low
341 detection probability, a closer line-spacing would be needed to reduce the number of missed
342 birds. But even this increased sampling effort does not guarantee the registration of all
343 individuals. Diefenbach et al. (2003) found that as many as 60% of the birds more than 50 m
344 from the observer were missed. However, detection probability is known to be dynamic and
345 differ by habitat (McShea and Rappole 1997, Schiek 1997), with lowest detection probability
346 in broad-leaved forests (Pacifici et al. 2008). Our results confirm these findings as they clearly
347 showed significant differences in the probability to detect a species between the four habitats
348 and the lowest EDR in beech forests. This finding has wider implications for bird surveys and

349 monitoring to be taken into account, by choosing the correct distance between walking routes
350 according to the EDR of that species that might be found in that habitat and which has the
351 lowest detection probability.

352 In our study, bird surveys conducted by DS were less time-intensive than TM.
353 However, using our survey design (which was not specifically designed for rare birds, e.g.
354 lacking many smaller transects or adjusted sampling, and therefore with no assurance of
355 sufficient detections for patchily-distributed species) the amount of effort taken for DS was
356 sufficient to calculate densities for only 15 out of 60 species detected. Additional reliable
357 density estimates would be possible if more birds were detected of those species. However,
358 these additional detections, especially of rarer bird species, would significantly increase
359 survey effort and therefore clearly reduce efficiency of DS. To calculate the abundance of a
360 bird species at least two registrations are required using TM, but at least 20 detections using
361 DS. Barraclough (2000) stated that the greatest drawback of DS is the number of detections
362 required. In an extreme case, if only a single pair of a less known bird species occurs in one
363 study plot, it has to be recorded several times, e.g. through repeated visits to the survey
364 location, before the precision of the abundance estimated by DS is adequate. If the bird
365 species is not well known, then pooling the distance data across groups of species with a
366 similar relationship between detectability and distance, as recommended by Buckland et al.
367 (2008), is not really possible. If confidence values are not needed, TM is more advantageous
368 for roughly estimating density of rarer birds. But DS is known to be less efficient in relatively
369 small study areas especially if densities of rarer birds must be sampled (Buckland et al. 2008).
370 However, if the species is rare, then both methods take more time; with TM, most sites will
371 give 'zero', so lots of sites will be needed, and using 5 minute-point counts might be more
372 efficient to detect rare species.

373 The absence of replication of our study in other landscapes might represent a
374 limitation to the number of species analysed and to general conclusions. However, our data

375 showed significant differences between the two methods, suggesting that results are still
376 sensitive to the method employed and demonstrating the need for recommendations on how
377 survey techniques can be further optimized, and ‘truth’ is to be found. If an exact statistical
378 estimation of the species’ density is needed, careful use of DS is more convincing as it
379 provides the coefficient of variation as well as the 95% confidence intervals for each
380 calculated density. Such statistical values for bird survey data are fundamental for science-
381 based and sustainable management (Walters 1986). Ideally 60 detections, or at least a robust
382 detection curve for each species, should be used to obtain precise DS estimates (Buckland et
383 al. 2001). If this number of detections cannot be reached, and when the survey design cannot
384 be adjusted to obtain a reliable detection curve, approximate or pooled data from other studies
385 or similar species can be used to estimate a detection curve and to be used to estimate
386 densities. Although those density values lack exact confidence values, for small study plots
387 this presents a pragmatic use. On the one side, a bird census using TM in habitats containing
388 species of low perceptibility could be optimized by walking routes spaced less than 50 m
389 apart which reduces the risk of missing elusive species. On the other side, a higher survey
390 effort increases the chance of double-counting for highly abundant and conspicuous birds.
391 Keeping TM flexible by adapting it to species and site specific requirements can be an
392 important advantage of TM though, and which distinguishes this method from other, more
393 standardized methods. However, this makes the method less comprehensible and therefore
394 less reliable especially for monitoring purposes as it is more driven by the observers’ right
395 assessment of local conditions.

396 The number of registrations at which a territory of a species will be counted has to be
397 treated with caution when using TM. From our results we cannot recommend a minimum
398 number of two or three registrations if eight effective visits of the study plot were conducted.
399 Instead, the number of registrations required to count a territory should be adjusted to the
400 species-specific detection probabilities. Based on the detection probabilities we can

401 recommend eight visits and a mean of four registrations to count a territory. However, if
402 detection probabilities of each species is known a species-specific treatment would be more
403 reliable. Generally, the missing confidence interval or any other statistically-based quality
404 assessment largely reduces the serious usability of TM for estimating densities and for
405 science-based management.

406

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414

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493 of spot-mapping data. *J Field Ornithol* 67:367-375

494 Table 1. Densities estimated using two bird survey methods in four different habitats. Bold type displays those differences when DS generated
 495 higher densities

Common name ^a	Scientific name ^a	Study site ^b	TM ^c 2 reg. ^d	TM 3 reg.	TM 4 reg.	TM 5 reg.	DS ^e	Δ DS.- TM 2 reg.	Δ DS.- TM 3 reg.	Δ DS.- TM 4 reg.	Δ DS.- TM 5 reg.	%CV ^f	95% CL ^g	No of detec- tions ^h	EDR ⁱ
Common Wood Pigeon	<i>Columba palumbus</i>	CF	5.8	5.6	3.9	2.9	1.7	-4.1	-3.9	-2.2	-1.2	24.4	0.7-2.8	56	133
Common Wood Pigeon	<i>Columba palumbus</i>	BF	3.6	3.4	2.6	2.2	1.7	-1.9	-1.7	-0.9	-0.5	38.2	0.9-2.5	36	110
Eurasian Skylark	<i>Alauda arvensis</i>	F	7.7	7.7	7.3	6.9	7.3	-0.4	-0.4	0	0.4	26.2	3.3-11.3	149	106
Tree Pipit	<i>Anthus trivialis</i>	OW	4.6	4.2	3.0	2.1	1.3	-3.3	-2.9	-1.7	-0.8	27.6	0.6-2.0	46	150
Eurasian Blackcap	<i>Sylvia atricapilla</i>	BF	6.2	5.2	3.6	2.4	3.9	-2.3	-1.3	0.3	1.5	27.8	1.8-6.1	36	79
Eurasian Blackcap	<i>Sylvia atricapilla</i>	CF	6.0	5.4	3.7	2.7	5.8	-0.2	0.4	2.1	3.1	21.1	2.0-9.6	47	80
Common Whitethroat	<i>Sylvia communis</i>	F	2.9	2.7	2.0	1.3	1.4	-1.5	-1.3	-0.6	0.2	34.5	0.7-2.1	20	100
Common Chiffchaff	<i>Phylloscopus collybita</i>	CF	2.3	2.1	2.1	1.9	1.6	-0.7	-0.6	-0.6	-0.4	33.9	0.8-2.3	32	111
Firecrest	<i>Regulus ignicapillus</i>	CF	22.7	13.5	10.4	8.1	27.6	4.9	14.1	17.2	19.5	20.6	9.4-45.8	34	29
Goldcrest	<i>Regulus regulus</i>	CF	12.1	8.9	6.0	4.4	18.2	6.1	9.3	12.2	13.8	29.8	8.3-28.1	31	34
Common Blackbird	<i>Turdus merula</i>	CF	8.1	7.9	6.0	4.6	2.1	-6.0	-5.8	-3.9	-2.5	29.1	0.9-3.3	53	117
Common Blackbird	<i>Turdus merula</i>	BF	6.4	5.6	4.0	3.0	3.9	-2.6	-1.7	-0.1	0.9	22.9	1.5-6.3	64	95
European Robin	<i>Erithacus rubecula</i>	CF	8.1	7.9	6.4	4.2	4.0	-4.1	-3.9	-2.4	-0.2	23.3	2.2-9.6	38	79
European Robin	<i>Erithacus rubecula</i>	BF	8.1	7.5	5.2	4.2	5.9	-2.2	-1.6	0.7	1.7	22.4	2.2-9.6	43	71
Great Tit	<i>Parus major</i>	OW	4.0	2.7	1.9	1.7	1.2	-2.8	-1.5	-0.7	-0.5	34.2	0.6-1.8	35	124
Coal Tit	<i>Parus ater</i>	CF	6.4	5.6	3.3	2.7	2.8	-3.6	-2.8	-0.5	0.1	25.8	1.1-4.5	31	86
Winter Wren	<i>Troglodytes troglodytes</i>	CF	13.5	12.7	12.1	10.2	5.1	-8.4	-7.6	-7.1	-5.1	21.6	1.9-8.3	91	105
Winter Wren	<i>Troglodytes troglodytes</i>	BF	4.6	4.2	3.0	2.6	3.7	-0.9	-0.5	0.7	1.1	24.7	1.5-5.9	31	73

Common Chaffinch	<i>Fringilla coelebs</i>	CF	26.6	26.2	25.4	22.3	15.3	-11.3	-10.9	-10.2	-7.1	14.5	4.4-26.1	181	101
Common Chaffinch	<i>Fringilla coelebs</i>	BF	24.6	23.4	20.3	16.1	26.5	2.0	3.2	6.2	10.4	19.9	8.5-44.6	209	71
Common Chaffinch	<i>Fringilla coelebs</i>	OW	6.8	6.1	4.9	4.4	4.6	-2.2	-1.5	-0.3	0.2	15.8	1.2-8.0	150	138
Yellowhammer	<i>Emberiza citrinella</i>	F	3.5	3.1	2.7	1.8	2.2	-1.3	-0.9	-0.5	0.4	29.4	1.0-3.4	42	94
Mean			8.8	7.8	6.4	5.1	6.7	-2.1	-1.1	0.4	1.6	25.8		66	95

496

497 ^aThe taxonomy followed ITIS (www.itis.gov).

498 ^bCF = coniferous forest, BF = beech forest, F = farmland, OW = open woodland.

499 ^cTM = densities (territories / 10 ha) estimated by territory mapping.

500 ^dreg. = Number of registrations used to count a territory.

501 ^eDS = densities (birds / 10 ha) estimated by distance sampling.

502 ^f%CV = coefficient of variation of the densities estimated by DS.

503 ^g95% CL = 95% confidence limits.

504 ^hNo. of detections = number of detections used to estimate densities by DS.

505 ⁱEDR = Effective detection radius [m] estimated by DS.

506

507 Table 2: Time required to survey birds in four different habitats of 25 ha area.

	Average survey time per visit (minutes)				Mean	508
	beech	coniferous	open	farmland	Mean	509
survey method	forest	forest	woodland			510
distance sampling	78	71	68	64	70	511
territory mapping	138	193	100	119	137	512

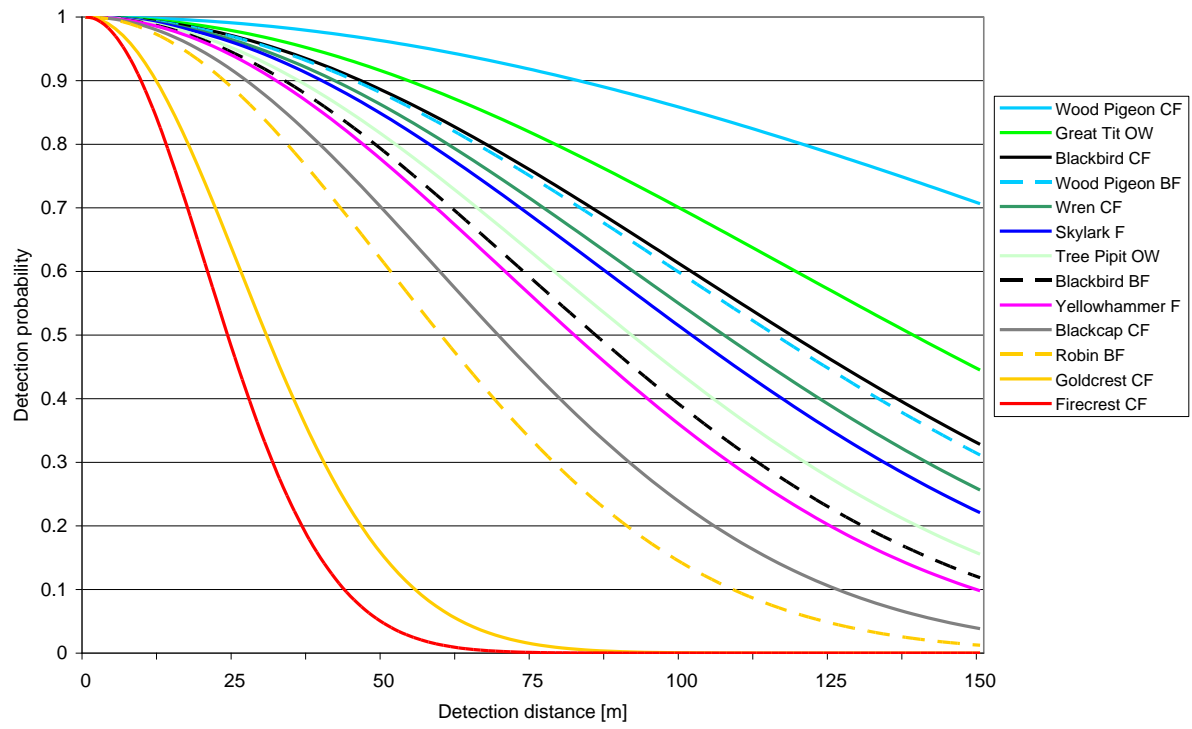
513 Figure legends

514

515 Fig. 1: Detection functions of 11 bird species. The curves show significant differences
516 between less and more detectable species. The truncation was set at a distance of 150
517 m. CF = coniferous forest, BF = beech forest, OW = open woodland, F = farmland.

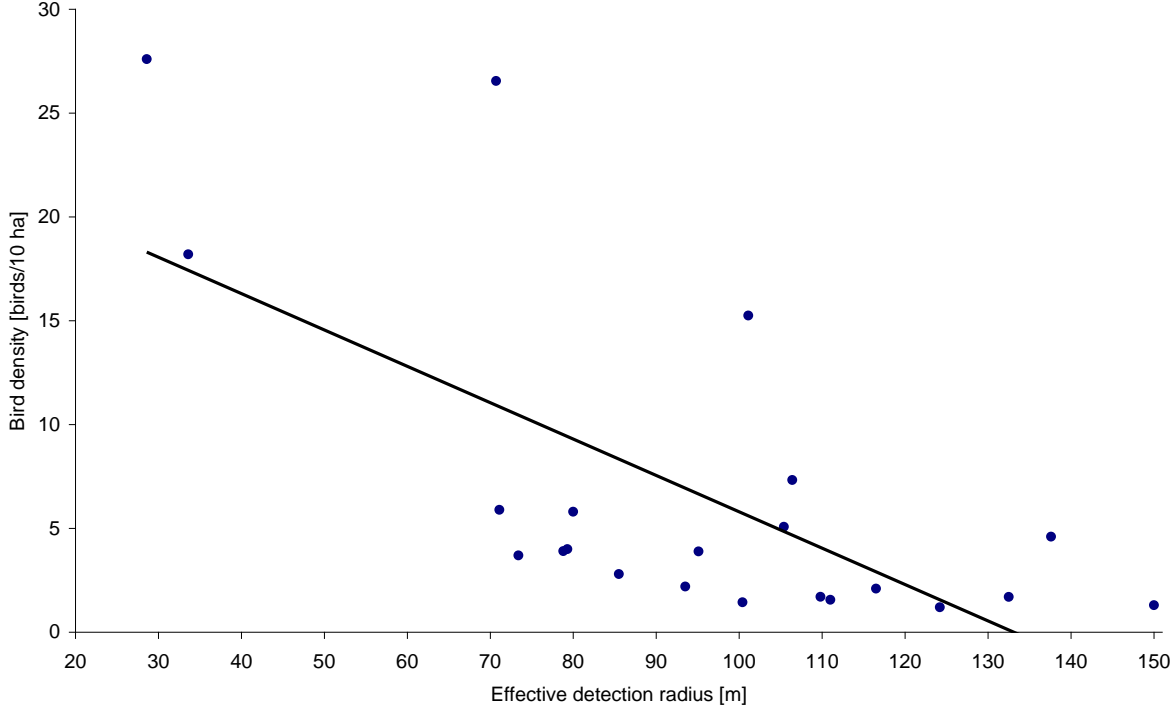
518 Fig. 2: Correlation between the detection probability depicted by means of the Effective
519 detection radius (EDR) and the density estimated by DS ($y = 23.3 - 0.175 x$).

520 Figures



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Gottschalk et al. – Figure 1



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Gottschalk et al. – Figure 2