Estimating relative densities of breeding birds by the line transect method. III. Temporal constancy of the proportion of main belt observations

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All observations are recorded in the line transect censuses, but, in addition, birds observed within 25 m from the transect are included in the *main* belt. The proportions of the main belt observations (MB) are used to estimate species-specific coefficients of detectability. These improve the efficiency of the transect method, for all the data can be used in estimating densities, and the variances of the estimates are also reduced.

In an experiment performed on the island of Åland in 1975, the same person censused 13.1 km forest transects eight times, and one 4.8 km field transect five times, at three stages of the breeding season and four different times of the day. MB is constant throughout the breeding season (June), but only if censuses performed at the same time of the day are compared. In forests, MB increases by almost 30 % from early to late morning. About a third of this increase can be accounted for by differences in the species composition of early and late morning censuses, but two-thirds arise from the decrease in bird activities that enhance detectability at a long distance. The changes in individual species are not significant (total sample 5000 observations, interpreted as pairs). No changes in MB were observed in the transect which ran through fields and coastal meadows.

Introduction

Methods of estimating relative densities of breeding birds by the line transect method have recently been improved (JÄRVINEN & VÄISÄNEN 1975). It is now possible to utilize those data which accumulate from the *supplementary* belt (= all observations which do not come from the *main* belt, 25 m on both sides of the transect), on the assumptions that (1) the proportion of the main belt observations (MB, 100MB = main belt percentage) describes the detectability of a species in a valid way, and that (2) the effect of increased distance on detectability can be approximated by simple models (see Järvinen & Väisänen 1975 for details). Two examples may serve to clarify the concept MB. Most ornithologists would guess that the MB of the Cuckoo Cuculus canorus must be among the lowest, because the 'coocoo' song of the male is easily identifiable and can be distinguished at a long distance. Accordingly, only a few main belt observations will accumulate per 100 individuals observed in the supplementary belt. On the other hand, the Woodcock Scolopax rusticola may be predicted to have a very high MB, because an individual is seldom seen during the usual census time in the morning unless it is nearly trampled on. The necessary parameters of the different models (JÄRVI-NEN & VÄISÄNEN 1975) are estimated from MB; if the same parameters can be used in large geographical regions, the variances of the density estimates for subregions will decrease appreciably LÄRVINEN 1976).

In this paper we shall investigate the constancy of MB during the breeding season and at different times of the day.

Materials and methods

Four transects were censused repeatedly during the summer of 1975 on the island of Åland (Ahvenanmaa; 60°N, 20°E). Five censuses were performed on transect IV, which covered mainly fields and meadows, but eight censuses were made on each of the three forest transects (I—III):

	Breeding season			
	Early (26.54.6.)	Midd le (8.618.6.)	Late (24.630.6.)	
Early morning (04-08)	3 I —IV	v I—IV	I—IV	
Late morning $(08-12)$	I—IV	ı—iv	I—III	
Afternoon (12—16)		I—III	_	
Evening (18—22)	—	I—III		

The censuses made on transects I—III (13.1 km) will be called 'forest censuses'; those made on transect IV (4.8 km) are the 'field censuses'. More details of these transects will be published later with data on the effect of season and time of day on the census of different species. All censuses have been made by the author Haila; thus no interobserver variation is present in the results.

An experiment of this kind is ideal

for the study of variation in MB with respect to our two temporal variables. However, we cannot compare the observed main belt percentages with, say, MB values from the mainland unless we recognize the fact that habitat structure affects MB appreciably. For example, suppose that one of the transects runs through the yard of a farm-house just at the midpoint of the territory of a Wheatear Oenanthe oenanthe. If Wheatears happen to be otherwise rare, almost all the observations of the species will be from the main belt and relate to this single individual. Or think of transect IV (fields): it is not surprising that very few forest birds have been observed in the main belt. Further, densities on Aland are among the highest in Finland, and the average MB of the expertimental censuses should be somewhat higher than on the Finnish mainland, since high densities of birds tend to increase MB (JÄRVINEN & VÄISÄ-NEN 1976). So we may expect that there will be deviations from the mainland

TABLE 1. Comparison between the main belt percentages (100*MB*) from the experimental censuses and those of censuses performed on the mainland of Finland (the material of JÄRVINEN & VÄISÄNEN 1975). The data are grouped according to the significance of the difference. A dozen species have been omitted because of the very small size of the samples (1—3 observations). A number of the species omitted have not been observed previously in Finnish line transect censuses, and comparisons would in any case have been impossible.

Significance	Experimental 100MB Higher Lower		
A. Not testable			
(small sample)	9	17	
B. Not significant	- 15	12	
C. P<0.05	5	2	
D. P<0.01	1	3	
E. P<0.001	5	0	
Total	35 spp.	34 spp.	

TABLE 2. Significance of the variation in MB in censuses performed at different hours and different stages of the breeding season.

Forest censuses Except censuses excluding those for which a	$\chi^2 = 28.68^{***}$ (d.f.=7)
corresponding field census was not made	$\chi^2 = 20.80^{***}$ (d.f.=4)
Field censuses	$\chi^2 = 2.92$ (d.f.=4)

MB, perhaps more towards higher than towards lower values. Thus the fact that in the experimental censuses 35 species have higher MB's and 34 have lower (Table 1) gives no reason to suspect that the present censuses differ in standard from those on the mainland.

Results

Altogether 4358 observations (interpreted as pairs) were made in the forest censuses, and 635 in the field censuses. The main belt percentage of the forest censuses (26.7 $\sqrt[9]{0}$) is higher and that of the field censuses $(18.7 \circ/6)$ is lower than is normal on the Finnish mainland (20.1 %, Järvinen & Väisänen 1975). MB varies highly significantly only among the forest censuses (Table 2). A set of forest censuses corresponding exactly to the field censuses also yields a highly significant value for the χ^2 statistic. However, MB does not vary between different stages of the breeding season if censuses made at the same time of the day are compared (Table 3): for forest censuses, $\chi^2 = 0.72$ (d.f.=2, P>0.5) in the early morning and $\gamma^2 =$

1.06 (d.f.=2, P > 0.5) in the late morning. In the field censuses no variation in *MB* is observed even when early and late morning are combined. It is thus the time of the day which causes temporal variation in *MB*; the late morning censuses differ clearly from all the others.

However, this does not warrant any inferences as regards individual species, because (1) trends in different species may balance each other, (2) variation in individual species may be of the same kind as that shown by all species together or (3) the temporal peaks of activity of different species may not coincide, and the observed differences may arise from the fact that different species (with different MB's) are observed in different censuses.

None of the species for which we possess sufficient data shows significant variation in MB (Table 4). There is no tendency towards high non-significant values of the test statistic, either, for eight values have a higher probability than 0.5, and eight have a lower one. The latter observation suggests that trends in different species do not balance each other. The trends of the rare

TABLE 3. The main belt percentage and its standard deviation (s) in the forest censuses, grouped with respect to the stage of the breeding season and census hours.

	Stage I	100 <i>MB</i> ± s Stage II	Stage III	Mean
Early morning	24.4±1.6	23.6±1.5	25.6±1.8	24.5
Late morning	32.3±2.2	32.1 ± 2.0	29.6 ± 2.0	31.3
Afternoon		27.1 ± 2.3	·	(27.1)
Evening		21 .9±1.9		(21.9)

TABLE 4. Significance of the variation of *MB* between censuses in different species. Rare species have been omitted; the species in parentheses do not strictly fulfil the conditions for a χ^2 test. N = total number of observations. All P > 0.05.

A Forest censuses (d.f. = 7)	
Parus major. N = 105	$\chi^2 = 6.93$)
All Parus spp., $N = 314$	9.49
Erithacus rubecula, N = 115	12.26)
Turdus merula, N = 119	5.33)
T. pilaris, $N = 145$	3.96
T. iliacus, $N = 181$	8.14
T. philomelos, $N = 160$	8.16)
All Turdus spp., $N = 540$	9.1 9
Sylvia borin, $N = 135$	11.56
(S. communis, $N = 89$	5.37)
Phylloscopus trochilus, $N = 362$	5.37
Regulus regulus, N = 82	3.48)
Anthus trivialis, $N = 195$	1.26
Fringilla coelebs, N = 786	6.10
Emberiza citrinella, N = 318	3.91
B. Field censuses (d.f. $= 4$)	
Alauda arvensis, N =249	5.97

species are unknown, but are unlikely to form an exception.

We then calculated the species-specific MB_i (for the *i*th species) from the forest data. If the MB_i values are really constant with respect to both of our temporal variables, all the observed variation in the total MB can be ascribed to variation in the species composition, i.e., MB will be higher late in the morning than early, because proportionately more low-MB species are active in the early morning. Consequently, if the expected number of main belt observations in the *j*th census is denoted by E_i ,

$$E_j = \sum_i MB_i N_{ij},$$

where N_{ij} = observations of the *i*th species made in the survey belt of the *j*th census.

The results (Fig. 1) reveal a nearly significant regression ($r = 0.80^*$, d.f. =

6), but the slope of observed upon expected values is 2.55, not 1.0 as required. Nevertheless, since the regression is significant, changes in species composition do account for a certain proportion of the variation in *MB*. The expected values for the early morning censuses are about 1.06 times as high as the observed values. The corresponding figure for the late morning censuses is 0.89. So, if the effect of the changes in species composition is eliminated, the ratio of late morning to early morning *MB* is as high as 1.06/0.89 = 1.18. This



FIG. 1. The relationship of expected (abscissa) and observed (ordinate) 100MB. The expected values are calculated on the assumption that the 100MB of a species does not change during the breeding season or between different times of the day. The line y=x is expected if the observed variation in 100MB can be entirely ascribed to variation in species composition. Symbols above (below) this line imply that the true 100MB values of the corresponding censuses are higher (lower) than the constant values used. ratio is meaningful — not based on random processes — because the two groups of censuses form tight clusters (see Fig. 1), which are significantly different from each other. The fact that the clusters are homogeneous supports the view that the seasonally constant total *MB* is not the result of a balance between subtle seasonal trends in individual species. So we can conclude that there is a considerable increase (18 %) in average *MB* from early to late morning, although the changes are too small to be demonstrated from data on single species (Table 4).

The rest of the difference between early and late morning is due to changes in species composition (the above regression). Since the ratio of the average MB's in the late and early morning censuses is 0.313/0.245=1.28, changes in species composition increase the main belt percentages, on an average, by a factor of 1.28/1.18=1.08 from early to late morning.

Discussion

We have observed that the proportion of main belt observations, MB, is constant throughout the breeding season. However, this is true only if all censuses are made at the same time of the day. Late morning censuses differ most from the others. These observations justify estimating main belt percentages from standard line transect censuses performed in any part of the breeding season, because one of the requirements of a standard census is that it has been performed in the early hours, beginning approximately at 4 o'clock a.m. (This starting hour varies, depending on weather conditions, transect lengths, the punctuality of the census-taker, and especially the geographical location of the transect.) So the present method of density estimation (JÄRVINEN & VÄIsänen 1975) is not more sensitive to seasonal variation than that developed by MERIKALLIO (1946); both are, of course, affected by the fact that the probability of detection of birds varies during the breeding season (e.g. SLAGS-VOLD 1973a, b).

Since *MB* increases from early to late morning, the validity of the estimates will be impaired if the census hours are extended in order to gather more data per day. Not all census methods are equally sensitive to the time of day. For example, ENEMAR (1959) observed rather small differences between the census results of different hours. However, there was a small decrease from the early morning hours. Similarly, FREMMING & SLAGSVOLD (1968) report variation in census efficiency with respect to census hours.

We shall discuss changes in density estimates in a later paper. Here we wish to point out that the increase in MB can be interpreted most naturally as indicating a change in the behaviour of the birds. Activities which make it possible to detect birds at a long distance are more common early than later in the morning. This is well illustrated by the forest data. In the main belt, about 8 % more individuals were observed in the early than in the late morning. In the supplementary belt, the corresponding percentage was over 50 %. So birds are almost equally easily detected at any hour before noon at a short distance, but their detectability at a long distance is greatly reduced. Such reduction of detectability was not observed in open country, because the MB of the field censuses did not change.

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Selostus: Linja-arviointimenetelmä pesimälinnuston paritiheyksien arvioinnissa. III. Lajin pääsarkahavaintojen osuuden vuorokauden- ja pesimäkaudenaikainen vaihtelu.

Linja-arviointimenetelmää sovellettiin vuosikymmeniä siten, että parit laskettiin 50 m leveältä pääsaralta, jonka perusteella arvioitiin tiheydet (paria/km²). Lisäksi laskettiin kaikki pääsaran ulkopuolelta havaitut linnut, mutta tutkimussarkaa (=pääsarka+apusarka) ei voitu johdonmukaisesti käyttää hyväksi.

Olemme kehittäneet menetelmää siten, että paritiheydet voidaan nyt arvioida tutkimussaran tuloksista (ks. osajulkaisuja I ja II: JÄRVINEN & VÄISÄNEN 1975 ja JÄRVINEN 1976). Tämä lisää menetelmän luotettavuutta tuntuvasti. Kullekin lajille on kehitetty kuuluvuuskerroin, jolla tutkimussaran parimäärä kerrotaan. Tiheys saadaan jakamalla tämä tulo reitin pituudella. Kuuluvuuskertoimet on johdettu lajin pääsarkaprosentista, joka tarkoittaa pääsaralla havaitun parimäärän osuutta kaikista laskennassa havaituista pareista.

Menetelmän soveltamisen kannalta on tärkeä tietää, vaihteleeko pääsarkaprosentti eri vuorokauden- ja pesimäkaudenaikoina tehdyissä laskennoissa. Tätä tutkittiin laskemalla Ahvenanmaalla samoja merkittyjä linjoja (yht. 17.9 km) pesimäkauden alussa, keskivaiheilla ja lopussa. Eri jaksoina laskentoja tehtiin aamulla, aamupäivällä, iltapäivällä ja illalla. Laskija oli aina sama. Kokonaislinnuston pääsarkaprosentti metsissä pysyi samana koko pesimäkauden, jos verrattiin samaan vuorokaudenaikaan tehtyjä laskentoja. Eri vuorokaudenajat sen sijaan poikkesivat metsälaskennoissa: pääsarkaprosentti oli keskimäärin 28 % korkeampi aamupäivällä kuin aamulla. Noin kolmanneksen kasvusta voitiin selittää johtuvan siitä, että laiikoostumus vaihteli eri laskennoissa. Kaksi kolmannesta noususta johtuu siitä, että lintujen havaitseminen kaukaa vaikeutuu aamupäivää kohti. Avomailla (peltoja ja rantaniittyjä) kokonaislinnuston pääsarkaprosentissa ei todettu vaihtelua.

Koska Suomen suuri linja-arviointiaineisto on kerätty aamulla, eivät vuorokaudenaikaiset pääsarkaprosenttimuutokset vaikuta lajien kuuluvuuskerrointen arviointiin.