Density estimates and their errors in line transect counts of breeding birds

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A method based on observations of a known population is presented for studying errors in line transect counts. The observation distances noted in a population count are applied to an imaginary line transect, where the observations are taken to represent average conditions. A comparison between true and estimated densities can then be made by applying formulae derived in the study. In this way estimates of the error due to the variations in the detection function are obtained.

The errors due to incomplete detectability on the central line can be studied by comparing the observed and actual number of birds in the study population. The results correspond to average conditions. The sampling error, which can be studied theoretically or with simulation experiments, is therefore not taken into account.

On the basis of different study methods, the error sources are divided into three groups. These can and should be studied separately, because the features and importance of the different kinds of error may vary. The classification of errors yields a framework within which the errors of line transect counts can be estimated.

Some illustrative computations are made in the case of the Wood Warbler. It is concluded that the most serious source of error is incomplete detectability at the central line.

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Introduction

The errors made in line transect counts have been discussed by listing different sources of error (Berthold 1976), by comparing the results of different methods or different observers (e.g. Järvinen et al. 1978a, b, Tiainen et al. 1980, Redmond et al. 1981), or by experimenting with lines in a known population (e.g. Haukioja 1968, Hildén 1981, Helle & Pulliainen 1983).

In the present study I introduce a new method of estimating errors made in line transect counts. As this method cannot be applied to all sources of error, the sources are classified according to the methods by which they can be studied. The classification of the sources of error provides a framework within which the errors made in line transect counts can be studied.

A method of studying the errors of line transect counts with the aid of a known population

The basic idea of the method is illustrated in Fig. 1. A count is made of a known population, the maximum observation distances of every unit being noted (Fig. 1A). These are then multiplied by a suitable factor, say ten, and distributed uniformly over an imaginary line transect (Fig. 1B). From such a distribution various results can be derived. For instance, from Fig. 1B one can conclude that, in the conditions of that day, on average 16 units out of 30 would be observed within a transect of width D+D.

Let the population of an imaginary transect belt be equal to the study population (in Fig. 1 this is true except that the transect population is multiplied by ten). Let. (be the true number of units in the study population. Further, let N be the number of units (birds, pairs) observed within the transect belt. Then. (-N birds are not observed because they are too far from the observer or, in other words, because the belt is too wide. In the following, the imprecise terms "birds" or "pairs" are used instead of "units". The precise definition of the unit as used in this paper is given in the section "Classification of sources of error".

Using a conversion formula, f can be estimated from N. The following method makes it possible to study the accuracy of such estimates.

Field observations from a study population are required (Fig. 1A). The greatest distance at which each bird was observed must be recorded. These sighting distances are then applied to an imaginary transect line (Fig. 1B). In the case of Fig. 1, the OULUN YLIOP:STO

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Fig. 1. Illustration of the main principle of the method presented in the paper. A count is made in a known population (1A), the greatest observation distances (d_1, d_2, d_3) for each unit are noted. The fourth bird is on the route but is not observed $(d_4=0)$. It is then assumed that the birds on an imaginary transect belt were similarly detectable. In Fig. 1B the birds are uniformly distributed on an imaginary line, each one of the units in Fig. 1A being represented by ten units in Fig. 1B. If the half belt width D equals d_1 , then all birds with $d=d_1$ are observed (filled circles in the lowest row). Most of the birds with $d=d_3$ are not observed (open squares in the uppermost row). Five birds out of ten will be observed within belt D+D, if $d=d_2$ (filled stars).

The greatest observation distance (d), line distance (1) and half belt width (D) are illustrated.

list of observations becomes d_1 , d_2 , d_3 . The fourth bird is not observed, i.e., its observation distance is zero. Such birds are not discussed in this section.

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d,

Let $\mathcal{N}(d)$ be the number of birds with the greatest observation distance equal to d (in Fig. 1B, $\mathcal{N}(d)=10$, if $d=d_2$, for instance). In line conditions, some of these birds cannot be observed from the line because their distance from it is larger than d; those located within the belt width d+d would be observed, however. Let N(d) be the number of such observations. This number is related to the width d+d of the belt where observations can be made. Let D+D be the full belt width of the transect. One then obtains as an average

 $N(d) = \mathcal{N}(d) \star d/D$

If in Fig. 1B $d_2=100$ m and D=200 m, then N(100) = 10 \star 100/200, i.e., 5 birds out of 10 are observed when d=100. As a simplification, let us assume that D is larger than any of the observation distances recorded for the study population.

The total number of the birds is the sum of birds with different observation distances,

 $\mathcal{N} = \sum_{\mathbf{d}} \mathcal{N} (\mathbf{d})$

where the sum is taken over all non-zero distances

recorded in the study population (In Fig. 1, d goes over d_1 , d_2 and d_3). The number of all the observations in the imaginary line transect is similarly a sum,

$$N = \sum_{d} N(d)$$

The mean observation distance along the imaginary transect becomes

$$\bar{d} = \frac{1}{N} \sum_{d} d N(d)$$

The variance of those distances is found from

$$s^{2}(d) = \frac{1}{N} \sum_{d} (d - \bar{d})^{2} N(d)$$

(1/(N-1)) instead of 1/N would be more correct).

Applying $N(d) = \mathcal{N}(d) d/D$ and denoting

 $S_{\nu} = \sum_{d} d^{\nu} \mathcal{N}(d) \text{ one can summarize:}$ 1) $\mathcal{N} = S_{0}$ 2) $N = S_{1}/D$ 3) $\bar{d} = S_{2}/S_{1}$ 4) $s^{2}(d) = S_{3}/S_{1} - (S_{2}/S_{1})^{2}$

These formulae all give values of parameters of



an imaginary transect with a half width of D. All of the parameters can be determined from function. I(d), which is the result of one count made on the known study population. It is assumed that the observation conditions of that count and of the line transect count are the same. As illustrated in the following section, it is not necessary to know parameter D.

Other quantities can be computed in the same way. The mean distance of the observation from the transect line is given by (formula not derived here, cf. Burnham et al. 1980:81; for the difference between distances l and d, see Fig. 1)

5)
$$\overline{l} = \overline{d}/2$$

The number of birds observed within a narrower belt of width L<D is determined as follows. Within that belt, birds with d>L are always observed because their observation distances are greater than the half belt width. For instance, in Fig. 1B let L=20 m, D=200 m, d_2=100 m and $\mathcal{N}(d_2)=10$. It appears that one bird with d₂ is observed within belt L+L. Generally, in belt L+L, the number of birds with d>L is

$$\sum_{d>L} \mathcal{N}(d) \ L/d$$

The number of other birds (as with belt D+D) is

 $\sum_{d\leqslant L} \mathcal{N}(d) \; d/D$

Thus the total number of birds observed within belt L+L is

6)
$$N_L = \sum_{d \leq L} \mathcal{N}(d) d/D + \sum_{d > L} \mathcal{N}(d) L/D$$

Eqs. 2 and 6 can be used to compute the relation between N_{I} and N.

The main formula of the present method is Eq. 2 or $N(d) = \mathcal{N}(d) d/D$. It describes the average number of birds on the imaginary transect. The main assumption is that the birds are uniformly distributed. A single transect result may deviate randomly from the computed values.

An illustration

If the length of the transect line is T, then the density quantity we wish to know is ... 1/(2DT). In King's method (Burnham et al. 1980:171), that quantity is estimated from N/(2dT). This is the conversion formula by which, in this particular method, the density estimate is derived from the observations. The relation between the estimate and the true value becomes N/d divided by \mathcal{M}/D .



Fig. 2. Daily values of mean observation distances on imaginary line transects. The distances are computed from late morning observations of 89 different counts on a Wood Warbler population.

If the mean of this relation does not equal 1, then King's method produces a systematic error. If the relation varies randomly, then there are random errors. The value of the relation is easily studied with the population observations by applying Eqs. 1, 2 and 3. Figs. 2 and 3 present values computed from 89 counts on a population of Wood Warblers Phylloscopus sibilatrix in 1974-80. The population is located in Kirkkonummi, some 30 km west of Helsinki. The results are based on observations made between 09.20 and 13.00 (10.20 and 14.00 in summertime). During each count, the observation distances of each pair (unit) was recorded. Most of the counts were made on subpopulations of ca. 10 pairs; some include the whole population, maximum ca. 30 pairs. The observations are from many years, so that they deal with a total of about 300 individuals.

Fig. 2 shows daily mean observation distances computed with the aid of Eq. 3. The values are valid for an imaginary line transect where the observation conditions and the behaviour of the birds (and of the observer) are the same as those of the population count.

The scatter of points in Fig. 2 is wild. In one case, in which all of the birds observed were sing-



Fig. 3. The ratio between the computed and actual densities on imaginary line transects. The parameters are computed from the data presented in Fig. 2. The densities are determined by King's method. The probability of observing a bird located on the central line is assumed to be 1.

ing unpaired males, the mean observation distance was 180 m. On the other hand, there are two cases with \bar{d} <20 m. The mean seems to vary around 90 or 100 m. During the time when birds have small young in the nest (about 20 June) their behaviour is not so open as is indicated by the reduction in observation distances (50—80 m). As the young grow, the distances increase up to 80— 90 m.

Fig. 3 presents the ratio (N/d)/(+/D), it, too, corresponding to the results of imaginary lines. Compared with Fig. 2, Fig. 3 shows fairly constant values. Thus, in spite of the wide variation in d, King's method gives a stable estimate of the density. However, there is a systematic underestimation of 25 per cent, as indicated by the mean value of the ratio (about 0.75). Varying conditions have only a moderate effect on the ratio. In May the values seem to be larger than in July. This rather small difference is evidently due to the different behaviour of the birds at the beginning and end of the breeding season. Assuming a linear detection function (computations given in the Appendix), one finds a theoretical value rather close to the mean of the values in Fig. 3. Thus the systematic error of 25 % can be explained theoretically.

Although King's method can be applied in estimating the density of the Finnish Wood Warbler population, the transect result must be multiplied by 1/0.75 or so in order to correct the systematic error of the method. According to the theory (see Appendix), a correction factor of 1/0.75 should always be applied if the detection function is linear. From Fig. 3, in the case of the Wood Warbler, a similar correction factor is found empirically with the aid of field observations, without any assumptions concerning the detection function.

Some variation in Fig. 3 is due to the small size of the samples. The detection function could have been different with a different routing. However, some extra noise variance does not impair the estimation of the error variance.

Other transect methods can be studied in a similar way by applying population counts.

Advantages and drawbacks of the method

Let us begin with some illustrative questions. In the population count, a bird may not be observed until it has been passed. How should the observation distance then be recorded? A bird is observed during a pause taken in order to ring fledglings in the nest. Should the bird be recorded or not? Two quiet birds are observed close to each other. Should they be counted as one or two pairs? If it is known from earlier observations that there are, in fact, two pairs, how should this been taken into account?

The answer to all these questions is clear. The observations should correspond to those made on an imaginary line transect. The same observation technique should be applied in the population counts as in line transect counts. If there are no pauses for ringing while the line is being censused, then the population count should be interrupted during a ringing pause. Observations made during that pause should not be taken into account and they should not affect or change other observations. The information on the study population should be used only as far as it could be obtained during a line transect census. The principle is to adhere to the sampling technique used in the transect work. For instance, the population discussed previously was not colour ringed because birds seen along a line transect cannot be identified by names like "red-blue on the left leg". Frequent captures may have made the birds more timid, too.

Here we have a clear advantage of the method. The effects of the observer and his behaviour are taken into account. On the other hand, a difficulty of the method is that the sampling technique must be properly simulated. It is not necessary to follow a straight line in the population count. However, the choice of the route should not depend on earlier observations or on the information about the population. Nor should the choice of the route cause systematic errors. For instance, the observer should not keep to roads or treeless places, if such routing is not applied in the transect work.

A Wood Warbler male may have many ter-

ritories or females. How should this be taken into account? In the present study population, polyterritorialism was often observed but never polygyny (there were a few possible cases). By the nature of the method, the effect of polyterritorialism is automatically taken into account, but the effect of polygyny is not included in the results. This is advantageous, because extra females are apparently rather rare in Finnish conditions.

A female Wood Warbler leaves the nest when the observer is at a distance of about 0.5 m. Thus, each square metre should be visited in order to cover the observation distances of each unit of the population. This is a disadvantage of the method. On the other hand, Wood Warblers with such short observation distances are rarely observed in real line transect conditions. Therefore the results will not be greatly changed if short observation distances are recorded as 0 m (= not observed). Hence, it is not necessary to visit every square metre of the study area.

Another problem with short-distance birds is the assumption of "circular flushing" (cf. Burnham et al. 1980:82). According to this assumption, the observations do not depend on the direction of the movement of the observer; the birds may "flush" independently of their location with respect to the line. If this assumption is significantly invalid, then both sighting distances and angles must be recorded. Corresponding transformations of the formulae are required.

Ideally, the relative contribution of short-distance birds to density parameters should be similar in population and line transect counts. Exact correspondence, however, is required only if one wishes to determine errors very accurately. In normal error studies, it is enough if reasonable estimates can be given.

The zero-distance birds. In theoretical computations one has to assume that all birds can be observed if they are close enough. In their "Summary of Important Points", Burnham et al. (1980:133) write "assure that all objects on the center line are detected". This is, at least in the case of the Wood Warbler, impossible. A bird on the line may easily be overlooked. For instance, two birds may be observed and recorded as one pair, though they in reality represent two pairs. Three males may be seen, but not simultaneously, so that only two are recorded. The problem cannot be avoided by using more sophisticated computation formulae. Therefore zero-distance birds are excluded from Eqs. 1-6. One solution to the problem of the zero-distance birds is to conclude that only relative density values are needed. Such values can be compared with each other if the systematic error of different transects can be assumed to be equal. However, this does

not remove the need for error estimation. Though the systematic error is assumed to be an unknown constant, it is nevertheless necessary to know the validity of this assumption and to estimate the random variations of the "constant".

The present method makes it possible to study the zero-distance birds. If a count in a population of 30 pairs results in 25 pairs, then 5 pairs were not observed. If the counting technique has been that of line transect counts, then these would presumably have been subjected to a similar underestimation. Thus the transect results should be multiplied by 30/25 in order to correct the error due to the zero-distance birds. Such correction factors may be slightly inaccurate, for it may be difficult to simulate the line transect technique closely enough. However, it is hard to conceive a better method.

Classification of the sources of error

Assume that the factors for correcting the error due to the zero-distance birds have been estimated. If such correction factors differ systematically from one, then the zero-distance birds cause systematic errors. If the correction factors vary around a mean value, then these birds cause random errors. As previously discussed, both the systematic and random errors can be studied by comparing the number of units observed with the actual size of the population. This requires that the true number of units is determined. Here, it becomes necessary to define precisely the concept of unit. For instance, in Figs 2 and 3 the unit has been a nesting female or an unpaired male. The aim of line transect counts has been defined as determination of the true density of such units of a nesting season. A discussion of different definitions of units can be found in Palmgren (1981:147).

If the true number of the units in the study population is not known, it is still possible to study the performance of the formulae used in the density computations. The systematic and random errors due to the variations of the detection function can be determined by applying Eqs. 1—6. The variations in the behaviour of the birds will be taken into account. However, the method implies that the birds of the study population are distributed uniformly over the imaginary line transect. Thus the method does not take into account the variations in line transect samples.

Thus, from the methodological point of view, we have three kinds of errors. There are 1) the sampling errors, 2) errors due to the variations in the detection function and errors generated by the density formulae and 3) errors due to the zero-distance birds.

The random sampling errors can, at least in

principle, be studied theoretically without any field observations (e.g. Burnham et al. 1980).

The errors of the second kind depend on the lateral detectability, in the terms of Järvinen 1978. In order to study these errors, it is necessary to know the detection function (or the lateral detectability) and its variations. In the method presented in this paper, the detection function is implicitly derived from the observations made in the study population. Hypothetical detection functions can be used, too (e.g. Järvinen & Väisänen 1975), but these allow only generalized conclusions.

The errors of the third kind depend on the basal detectability. If this is complete, then there are no such errors. These errors are normally not studied or they are studied only in connection with other error types. As presented, the basal detectability and its effects can be studied with the known population, if the true number of units is known.

Thus we can present a practical division of the error sources. Errors due to the zero-distance birds, or those associated with the basal detectability, could be termed basal detectability errors. They are studied independently of the errors of the second kind. These could be termed lateral detectability errors. They can be studied with Eqs. 1—6. All the other errors could be called sampling errors. In this classification the measurement errors are grouped with sampling errors.

The following crude characterization gives another view of the present classification. The basal errors are due to the incomplete efficiency of the observer in detecting birds. The lateral errors are similarly due to that incomplete efficiency, but should be corrected by the method used in the density computations. Thus the lateral errors, if they exist, are due to the method. The sampling errors are mainly due to the choice of the transect lines.

In summary, the error classes will be as follows

Samp	ling
(incl. meas	urement)
systematic	random
······	
systematic Late	ral random
-	
Basal	
systematic	random

Discussion

Separate study of the error sources is a practical solution. Large samples are required if the sampl-

ing error is studied in field conditions, since the variations in the location of birds in different nesting phases should be properly represented. It is thus more practical to study the random sampling errors theoretically. The field studies can then concentrate on other error classes.

It is often argued that transect results are sensitive to a variety of factors. The following list is from Dawson (1981): bird species, season, habitat, time of day, weather, observer. It seems that random sampling errors are of minor importance here. Their theory is rather well known, and their contribution can be made smaller by increasing the sample size. If the formulae used in the density computations are properly chosen, then the random lateral detection errors seem to be rather small (Fig. 3). Similarly a correct choice of the counting period seems to prevent systematic lateral errors (Fig. 3). Thus the most serious error is most probably the basal error, i.e. the one due to the zero-distance birds. This conclusion is in agreement with Burnham et al. (1980:132): "The most critical assumption is that if an object is on the line of travel, it will be seen with probability 1". Thus it is desirable that more work is done on that error. The method discussed in this paper is easy to use. One need merely count the units of a known population and compare the result with the actual population size. The only aim is to study how the birds would be observed on the line of travel, i.e., at zero distance. If the bird is observed at a greater distance, then it is assumed that it would have been observed on the line of travel. If the bird is not observed in the population count, it will not be observed on the line of travel. This requires that the population is known and that the conditions of the transect count are properly simulated. On the other hand, the population count does not require an experimental transect line. One can walk along any route, so that the probability of observing each unit is maximized, as if it was on the transect line. In this way the number of birds on the line becomes larger and so the study of the error is based on a larger sample.

It is to be noted that the present classification of errors is not based on factors generating errors. The lateral error (Fig. 3), for instance, is affected by many factors, e.g. the changing behaviour of the birds during the nesting cycle; different nesting cycles in different years; different nesting places with a different topography. In the case of Fig. 3, the weather changed between both days and years. The observation technique changed (was developed) during several years. The counting time, the late morning, is a time when the behaviour of males shows large differences in different phases of the nesting cycle. All of these factors have been taken into account in the results derived from Fig. 3.

The classification is based on the methods by which the errors are studied. The methods may be different in different bird species, so that the classification may vary from species to species.

Appendix

The bias of King's method in the case of a linear function. The detection function, g(1), is related to the probability of observation. If detectability is complete, then the value of the function is 1. If no birds can be observed, then the value is zero. The function depends on the distance, 1 (for the definition of 1 see Fig. 1 in the main text). If the detectability is complete at the line then g(0)=1. If no birds can be observed at a distance of 100 m, then g(100)=0. If within the transect belt 0<1<D all birds can be observed, then g(1)=1, 0<1<D. In that case, the total number of birds is formally given by

$$\mathcal{N} = \mathcal{M}_D \int_0^D g(\mathbf{l}) d\mathbf{l}$$

where \mathcal{N} is the true number of birds within the transect. In the case of a linear detectability function the observation efficiency decreases linearly until some limit, say

D. The function has the form of g(l)=1-l/D, 0<l<D. The total number of birds observed is given by

$$N = \mathcal{N} D \int_{0}^{D} g(l) dl$$

It follows that N = M/2.

The mean distance of the observed birds from the line is

$$\bar{l} = 1/N \star \mathcal{M}D \int_{0}^{D} l g(l) dl,$$

which gives $\overline{l}=D/3$. The mean observation distance \overline{d} is given by $\overline{d}=2\overline{l}$, because $\overline{d}=2\overline{l}$ (cf. main text, Eq. 5). Thus $\overline{d}=2D/3$.

Thus half of the birds are observed and the mean observation distance is given by 2D/3. Assuming that the sample is so large that the random errors are negligible, one obtains a value of 0.75 for $(N/d) / (\mathcal{W}/D)$. This figure is thus based on the assumption that the detection function is linear and is to be compared with values derived from real detection functions (Fig. 3 in the main text).

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Selostus: Linjalaskennan virheenarviointi

Kirjoituksen lähtökohta on esitetty kuvassa 1. Tutkimus perustuu laskentoihin, jotka on tehty tunnetussa populaatiossa merkiten muistiin kaikkien sen yksilöiden havaittavuus. Laskennat tehdään jäljitellen linjalaskennan tekniikkaa. Reitin ei kuitenkaan tarvitse olla suoraviivai-

nen. Sitä vastoin sen on katettava koko populaatio, jotta sen kaikkien yksiköiden (lintu, pari) havaittavuus voitaisiin selvittää. Kuvaan 1A on merkitty kolmen linnun maksimaaliset havaintoetäisyydet, esim. $d_1=195$ m, $d_2=100$ m ja $d_3=20$ m. Neljättä lintua ei ole havaittu, vaikka se on ollut reitillä. Sen havaintoetäisyys on 0 m. Seuraavaksi oletetaan, että kuvitellulla linjalla linnut olisivat olleet havaittavissa juuri samoilta etäisyyksiltä, joko d_1 , d_2 tai d_3 ja että kaikkia näitä olisi samassa suhteessa linja-alueella kuin on tutkimuspopulaatiossa. Kuvassa 1B on osa kuviteltua linjaa, jonka varrelle on tasaisesti sijoitettu populaation 1A lintuja d_1 , d_2 ja d_3 , kullekin 10 edustajaa. Linjasaran leveys on D+D, esim. D=200 m. Linjan vetäjä ilmeisesti havaitsisi kaikki pitkän havaintoetäisyyden omaavat linnut (mustat ympyrät, käytännössä nämä ovat esim. pariutumattomia sirittäjäkoiraita). Sitä vastoin 20 metrin linnuista havaittaisiin linjalle vain 1 (musta neliö), vaikka niitä linjan alueella on 10. Kaikkiaan 30:stä linnusta havaittaisiin 16 (mustat neliöt, tähdet ja ympyrät). Tällä tavalla voidaan tutkia esim. laskentamenetelmien tehokkuutta. Kirjoituksessa esitetään joukko kaavoja, joiden avulla laskelmat voidaan tehdä.

Esimerkinomaisesti sovelletaan kirkkonummelaisessa sirittäjäpopulaatiossa vuosina 1974–80 tehtyjen 89 laskennan tuloksia. Parhaimmillaan yhdessä laskennassa on tutkittu lähes 30 parin havaittavuus. Yhteensä tutkimuksen aikana havaintoja on tehty n. 300 eri yksilöstä pesinnän kaikissa vaiheissa. Laskenta-aika on tietoisesti ollut linjalaskennan kannalta hankala, klo 10.20–14.00 kesäaikaa.

Kuva 2 esittää kaikkien sirittäjien keskimääräiset havaintoetäisyydet siten kuin ne kunakin päivänä olisi havaittu kuvitellulle havaintolinjalle. Tulokset perustuvat 89 populaatiotutkintaan. Mukaan ei ole otettu niitä lintuja, joiden havaintoetäisyys on 0 m, s.o., joita ei havaita missään olosuhteissa. Jonakin kertana keskimääräinen havaintoetäisyys olisi ollut 180 metriä, jonakin vain 20 m. Suuret erot kuvaavat havaittavuuden suurta vo-htelua. Kuva 3 näyttää, mitkä olisivat olleet vastaavat tiheysarviot verrattuna todelliseen tiheyteen. Tiheysarvot on ajateltu laskettavaksi Kingin menetelmällä. Samalla tavalla ja samalla aineistolla voitaisiin tutkia myös muita menetelmiä, kuten Merikallion menetelmää. Arvo 1 vastaa oikeata tulosta. Yleensä kuvan 3 pisteet ovat välillä 0.5–1. Vastaavasti laskentojen tulokset olisivat olleet 50–100 % todellisesta. Keskimäärin tulos on 75 % (kun linnut ovat tasaisesti jakautuneet ja 0-metrin lintuja ei ole otettu mukaan). Vaihtelu on verraten vähäistä. Linjalaskennan tulos on siis hämmästyttävän vakaa, keskimäärin se aliarvioi 25 %. Tämä tulos on kuitenkin voimassa vain Kingin menetelmälle ja vain sirittäjälle. Liit teessä kuitenkin osoitetaan, että 25 %:n aliarvio on sangen yleisin ehdoin voimassa Kingin menetelmälle.

Edellä linnut on ripoteltu tasaisesti laskentareitille. Luonnossa voi kuitenkin joku reitti sattumalta olla tyhjä, joku taas ylitiheästi asutettu. Tätä otantavirhettä voidaan tutkia teoreettisesti. Tulos (sampling error) on yhdistettävä edellä selostettuun virheeseen (lateral error).

Vielä on otettava huomioon ne linnut, joita ei havaita edes lähietäisyydeltäkään. Näiden aiheuttamaa virhettä voidaan tutkia populaatiolaskentojen avulla. Jos esim. 30 linnun populaatiosta voidaan löytää vain 25, voitaneen olettaa, että samoin olisi käynyt linjalla: 30:stä linnusta 5 olisi jäänyt havaitsematta vaikka kaikki linnut olisivat olleet aivan linjaviivan lähellä. Kirjoituksessa arvioidaan, että tämä virhelähde (basal error) on linjalaskennan kannalta kaikkein pahin (ainakin sirittäjää laskettaessa).

Näin siis virhelähteet jakautuvat kolmeen eri tyyppiin, joita kaikkia voidaan ja on syytäkin tutkia erikseen. Kuva 3 esittää vain yhtä tyyppiä, sen lisäksi on vielä selvitettävä kaksi muuta. Jokainen virhetyyppi jakautuu vielä kahteen osaan, satunnaiseen ja systemaattiseen. Lopullinen virhearvio saadaan yhdistämällä kaikkien virhelähteiden vaikutukset.

Kirjoituksen lopputulos on suunnitelma, jonka mukaan linjalaskennan virhettä voidaan tutkia.

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