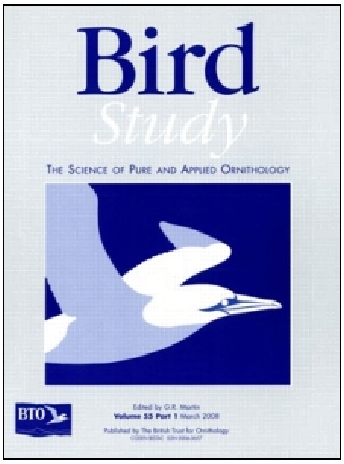

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Estimation of bird distribution based on ringre-encounters: precision and bias of the division coefficient and its relation to multi-state models

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Estimation of bird distribution based on ring re-encounters: precision and bias of the division coefficient and its relation to multi-state models

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Capsule The division coefficient is an estimate of the proportion of ringed birds migrating to different destination areas taking into account area-specific re-encounter probabilities.

Aims To explore precision and bias of the division coefficient method by a simulation study and to compare the approach with multi-state models.

Methods In a simulation study true and estimated division coefficients were compared. The division coefficient method was mathematically compared with the multi-state model.

Results The estimated division coefficients seemed to be unbiased if the assumptions were met. The precision decreased if the bird distribution became similar in both bird groups and when difference between area-specific re-encounter probabilities increased. A bootstrap method to assess precision is presented. The estimates from the division coefficient method equal the maximum likelihood estimates in a multi-state model including only one time interval.

Conclusion Before applying the division coefficient method or a multi-state model to real data a simulation study should be conducted in order to explore the behaviour of parameter estimation. The division coefficient method with the bootstrap confidence intervals is an easy alternative to a multi-state model with one time interval when the bird distribution between destination areas (e.g. migratory connectivity) alone is of interest.

Making inferences from re-encounters of ringed birds about their migration patterns is difficult because of underlying spatio-temporal heterogeneity in re-encounter probabilities (Coulson 1966, Davis 1966, Snow 1966, Perdeck 1977, van Noordwijk 1995). Several different approaches have been developed to overcome this problem. Sometimes relative measurements are used, for example, the proportion of a group of birds migrating to a specific area relative to a reference group, assuming that the probability of reporting ringed individuals from all groups is the same (Lokki & Saurola 1987, 2004, Siriwardena *et al.* 2004, Kania 2006). Recently research has focussed on multi-state mark–recovery models (Brownie *et al.* 1985, Schwarz 1993, Thorup & Conn 2009) and state–space models (see review by Patterson *et al.* [2007]) in order to disentangle re-encounter probability, survival and proportion of birds migrating to different destination areas. Specific software was developed for estimation of parameters in such models, for example, SURVIV (White 1992), MARK (White & Burnham 1999) or M-SURGE (Choquet *et al.* 2004).

Less attention has been given to the method proposed by Busse & Kania (1977) and Kania & Busse (1987), which separates the proportion of birds migrating to different destination areas from area-specific re-encounter probabilities, by estimating the *division coefficient* (Fig. 1).

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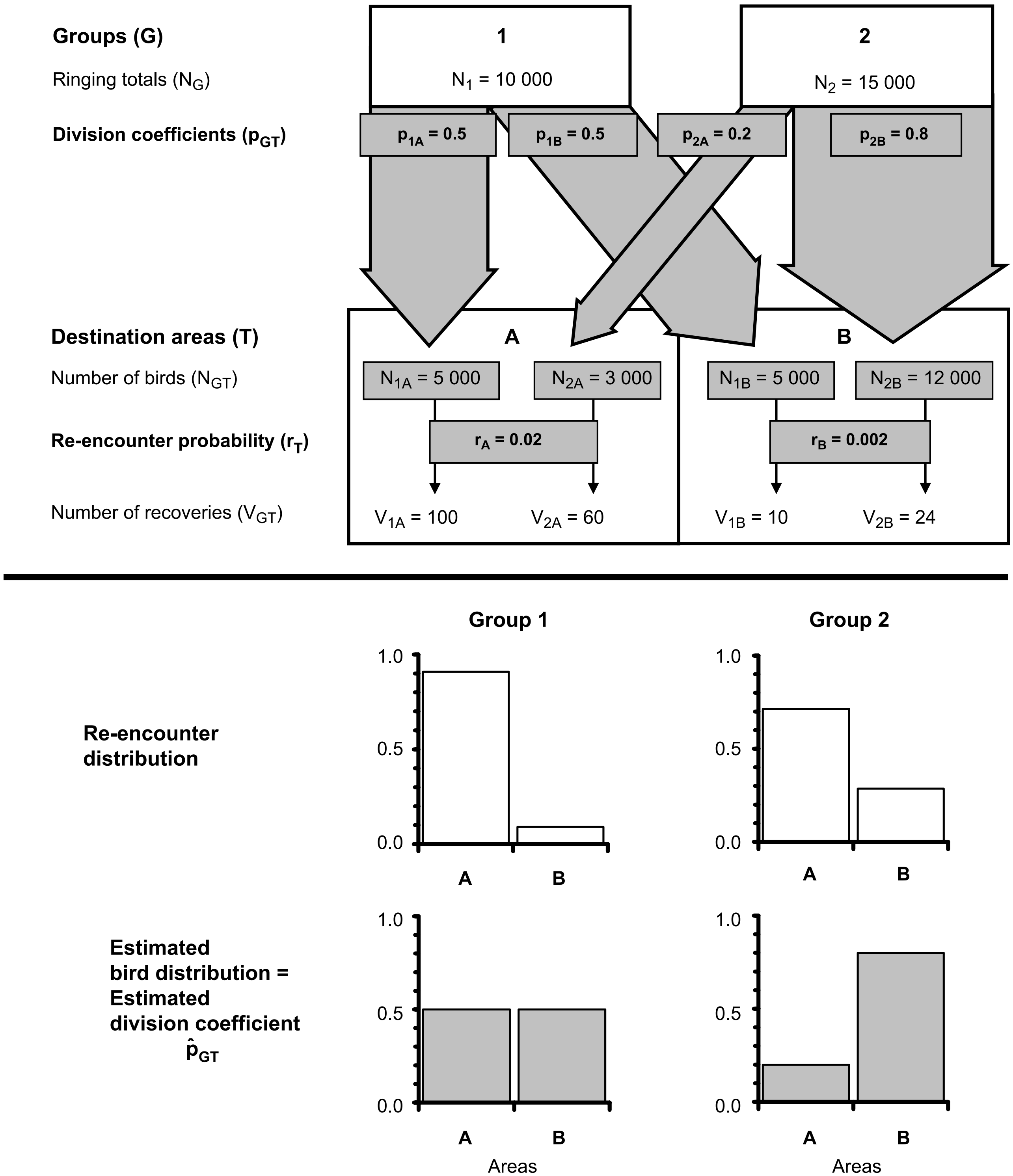

Figure 1. Illustration of the division coefficient concept. An idealized example of the distribution of two groups of ringed birds on two destination areas. N_G, number of ringed birds per group; p_{GT}, proportion of birds of group G migrating to area T (division coefficient); r_T, re-encounter probability (probability of recovery *sensu lato*) in area T; V_{GT}, number of re-encounters of group G in area T; N_G and V_{GT} are observed data (not shaded); r_T and p_{GT} are unknown parameters (shaded grey) that can be estimated by the division coefficient method or by a multi-state model. Redrawn after Kania & Busse (1987).

Although this approach is very intuitive and easier to apply than the aforementioned models, it has not become commonly used in re-encounter analyses, possibly because an estimator of uncertainty, such as standard error or a confidence interval, was not available.

In this work we explore the performance of the division coefficient based on simulated data in order to assess the violation of the assumptions underlying the concept and the requirements needed for precise estimations. We then present a non-parametric bootstrap method for obtaining confidence intervals. Finally, we show that the division coefficient is mathematically related to the multi-state model.

We use the term 're-encounter' for recoveries of dead birds, live recaptures and re-sightings, as proposed by Thomson *et al.* (2009).

DIVISION COEFFICIENT CONCEPT

Combining ringing and re-encounter data of different groups of birds (for example, local populations, migration waves, sex classes, sometimes species), for which it can be assumed that they experience equal re-encounter probabilities in shared destinations or stopover areas, enables the estimation of those probabilities and the proportion of birds within each group migrating towards those areas. The proportion of birds from group G potentially migrating (i.e. including birds that die before or during migration) towards destination T is called the division coefficient (Busse & Kania 1977, Kania & Busse 1987) (Fig. 1). The term division coefficient is synonymous with the term migration rate used in the mark–recapture framework.

In the division coefficient concept, the number of ringed birds N_G per group G and the number of recovered birds V_{GT} of group G in destination area T are related in a system of linear equations. For an example of two groups and two destination areas (Fig. 1), such a system of equations is:

$$N_1 = V_{1A}\hat{x}_A + V_{1B}\hat{x}_B \qquad (1)$$
$$N_2 = V_{2A}\hat{x}_A + V_{2B}\hat{x}_B.$$

We denote $\hat{x}$ and $\hat{r}$ as estimates of x and r. x_T is the number of birds ringed necessary for obtaining one re-encounter, i.e. the inverse of the re-encounter probability in area T:

$$x_T = \frac{1}{r_T}. \qquad (2)$$

Note that r_T (re-encounter probability) is defined as the ratio of the number of birds re-encountered in the area T to the number of ringed birds belonging to the group migrating to the area T.

There exists one exact solution for $\hat{x}_T$ if the number of groups equals the number of destination areas, and a least square solution can be found if the number of groups exceeds the number of destination areas. $\hat{x}_T$ is not identifiable if the number of groups is lower than the number of re-encounter areas and if the division coefficients are equal between the groups (Busse & Kania 1977, also see later). The division coefficient can be estimated by the ratio

$$\hat{p}_{GT} = \frac{V_{GT}\hat{x}_T}{N_G} \qquad (3)$$

and the estimate of the re-encounter probability is

$$\hat{r}_T = \frac{1}{\hat{x}_T}. \qquad (4)$$

PRECISION AND BIAS OF DIVISION COEFFICIENT

In order to assess precision, bias and requirements of the division coefficient estimate, we simulated data based on different true division coefficients and re-encounter probabilities. We considered two destination areas (A and B) and two groups of birds (1 and 2). We chose three proportions in re-encounter probabilities (r_A/r_B = 1, 3 and 6 respectively): with r_A = 0.03 and r_B = 0.03, 0.01 and 0.005. Within each proportion of re-encounter probability, numbers of re-encounter data (V_{1A} ,V_{1B}, V_{2A}, V_{2B}) were simulated based on different underlying division coefficients. The division coefficient for Group 2, p_{2A}, was set to 0.5, 0.7 or 0.9 (p_{2B} was then 0.5, 0.3 or 0.1 respectively), whereas for Group 1 p_{1A} varied from 0 to 1 with step 0.02. For each combination of true parameters we simulated 5000 sets of data.

Data simulation was done in two steps: first, for each group G we simulated the number of birds migrating towards area A (N_{GA}) as binomially distributed with given division coefficients (p_{GA}). The number of birds migrating towards B was then obtained by subtracting N_{GA} from N_G:

$$N_{GA} \sim \mathrm{binom}(N_G,\ p_{GA}) \qquad (5)$$
$$N_{GB} = N_G - N_{GA}.$$

Then the number of re-encounters for each group G within A and B were randomly drawn with the re-encounter probabilities r_A and r_B.

$$V_{GA} \sim \text{binom}(N_{GA}, r_A) \qquad (6)$$
$$V_{GB} \sim \text{binom}(N_{GB}, r_B).$$

The numbers of released birds of each group, N_1 and N_2, were set to 15 000 each in every simulation.

For each simulated set of data we estimated the division coefficients $\hat{p}_{1A}$ and $\hat{p}_{2A}$ and the re-encounter probabilities $\hat{r}_A$ and $\hat{r}_B$ by solving Equation system 1 and using Equations 3 and 4. Then the means and the 0.025 and 0.975 quantiles of the 5000 estimated division coefficients and re-encounter probabilities for each parameter constellation were calculated. The simulations and estimations were done in R 2.6.1 (R Development Core Team 2007).

The simulations show that the estimates of division coefficient and re-encounter probabilities are accurate and precise if differences in true division coefficients between the two groups are large (Figs 2 & 3). The precision increases (narrower 95% range of estimates) and bias decreases with increasing difference in division coefficient between the groups. If division coefficients of the groups are similar, the estimates are very sensitive to random variation in the data, and if the division coefficient is equal in both groups, the equation system is not solvable. Precision decreases and bias increases with increasing difference of the re-encounter probabilities between destination areas (Fig. 2).

FURTHER REQUIREMENTS AND ASSUMPTIONS

Beside a large difference in division coefficient between the groups, a large enough number of ringed and recovered birds are required to get precise estimates. The bootstrap confidence intervals (see later) can be used as a guideline about how precisely the division coefficient can be estimated based on the data at hand.

However, there are further assumptions whose violation results in biased parameter estimates, and that are therefore more critical (see detailed discussion in Kania & Busse [1987]). They should be checked carefully before applying this method. First, different groups must have equal re-encounter probabilities (r_T) within destination areas, otherwise the estimated division coefficient can be biased (see Fig. 4 for an example). In practice this assumption is difficult to test, but is likely to be best fulfilled if ecologically similar groups are used. For instance, we divide birds into different migration waves or neighbouring local populations, rather than into different age classes, since survival is usually lower in first year birds than in adults and therefore the probability of re-encountering an individual within a given time interval is lower for juveniles than for adults. But care must be taken when combining data from different ringing schemes, because re-encounter probability can also depend on the address on the ring (Sales 1973). Secondly, the re-encounter probabilities and bird distribution should not change within the time of the study. Thirdly, the re-encounter probabilities must be uniform within each destination area, requiring a careful selection of the destination areas. Factors producing spatial heterogeneity in re-encounter probability, such as hunting regimes, human cultural factors, human population density, education, income level or habitat have to be considered. Fourthly, all destination areas together should include the whole area where the ringed birds can migrate to, because Equation system 1 is based on the assumption that the division coefficients of each group sum to one. However, when we have at least two groups migrating exclusively to two known destination areas (A and B), it is possible to estimate the division coefficients for further groups consisting of birds migrating to A, B and C, whereas C can be an area without or nearly without re-encounters. In this case, the re-encounter probabilities have to be estimated for those groups migrating exclusively to the areas A and B. Next this estimated re-encounter probability can be used for estimating the proportion of birds that migrate to area A and B for the further groups (division coefficients). Then subtracting these division coefficients from one gives the estimation of the proportion of birds migrating to area C from these groups (Busse & Maksalon 1978).

APPLICATIONS

The method was developed to estimate proportions of birds from consecutive migration waves going to various wintering areas, for Chaffinches *Fringilla coelebs* (Kania 1981) and used in a similar way for Song Thrushes *Turdus philomelos* (Busse & Maksalon 1978). The division coefficient method is especially useful in analyses of ring re-encounter data resulting from intensive ringing in places on the migratory route of populations that differ in their proportions of individuals migrating to various (neighbouring) wintering grounds. Such conditions are met by many field stations in central Europe through which relatively close-breeding north European populations pass

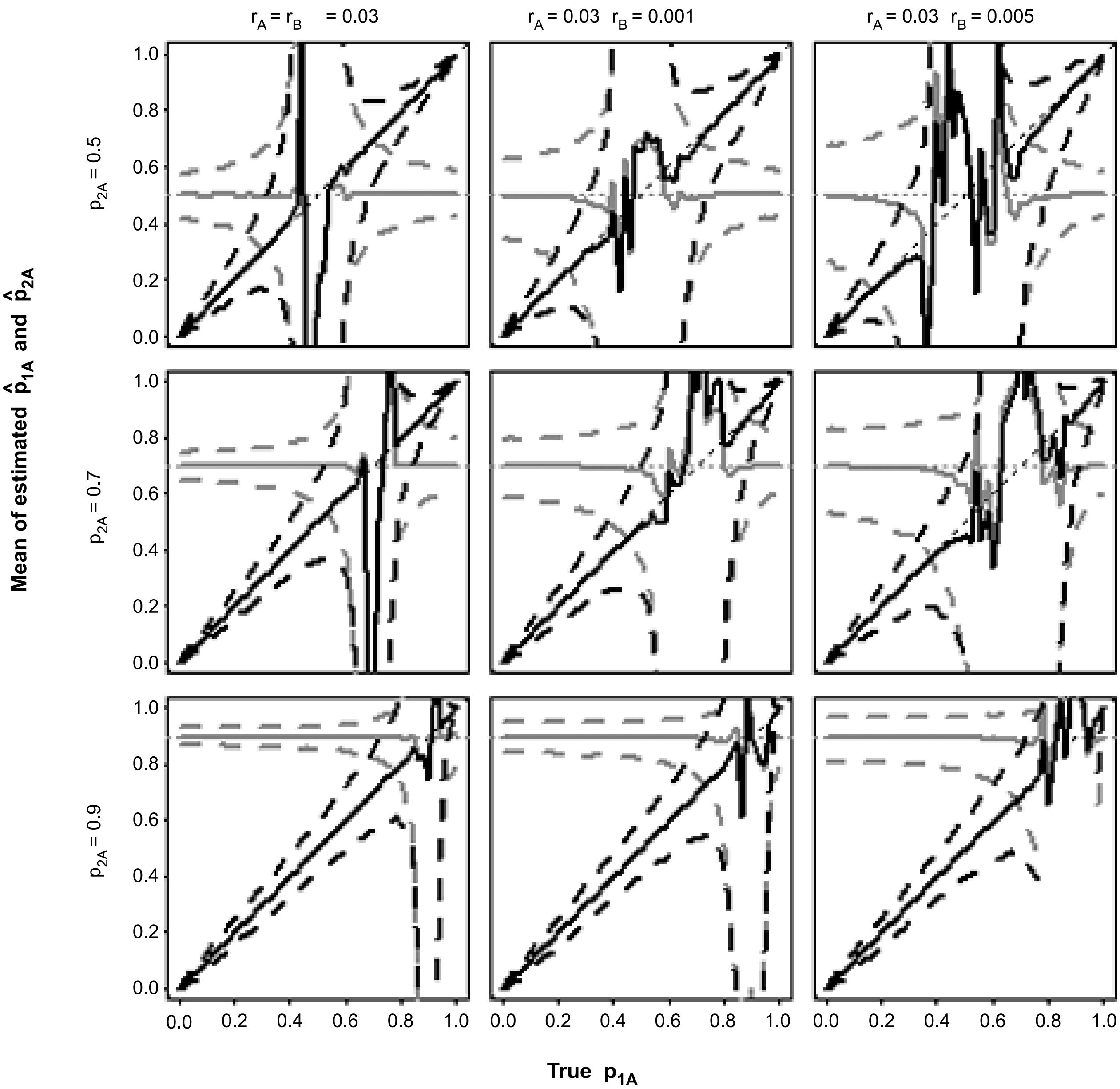

Figure 2. Precision and bias of the estimated division coefficient $\hat{p}_{1A}$ and $\hat{p}_{2A}$ depending on the difference between true p_{1A} and true p_{2A} and the proportion of true re-encounter probability r_A to r_B. Bold lines, means of 5000 estimated division coefficients $\hat{p}_{1A}$ and $\hat{p}_{2A}$; broken lines, 0.025 and 0.975 quantiles of these estimates; dotted lines, true values p_{1A} and p_{2A}; black, group 1; grey, group 2; true p_{2A} is set to 0.5, 0.7, or 0.9; true p_{1A} varies from 0 to 1 (by step 0.02). Results are shown for three different ratios for re-encounter probabilities. When no bias is present the estimated $\hat{p}_{1A}$ lie around a straight diagonal line and estimated $\hat{p}_{2A}$ around a horizontal line at the height of true p_{2A}.

(Petryna 1976, Busse & Maksalon 1978, Kania 1981, Busse 2001, Remisiewicz 2001, 2003).

The approach can also be used for comparing breeding populations wintering in different proportions in distinct parts within the wintering grounds, e.g. for European Storm Petrels *Hydrobates pelagicus* wintering along the western coasts of Africa (Fowler 2002). Similarly, the division coefficient method can also be used to compare the breeding distribution of birds ringed on wintering grounds.

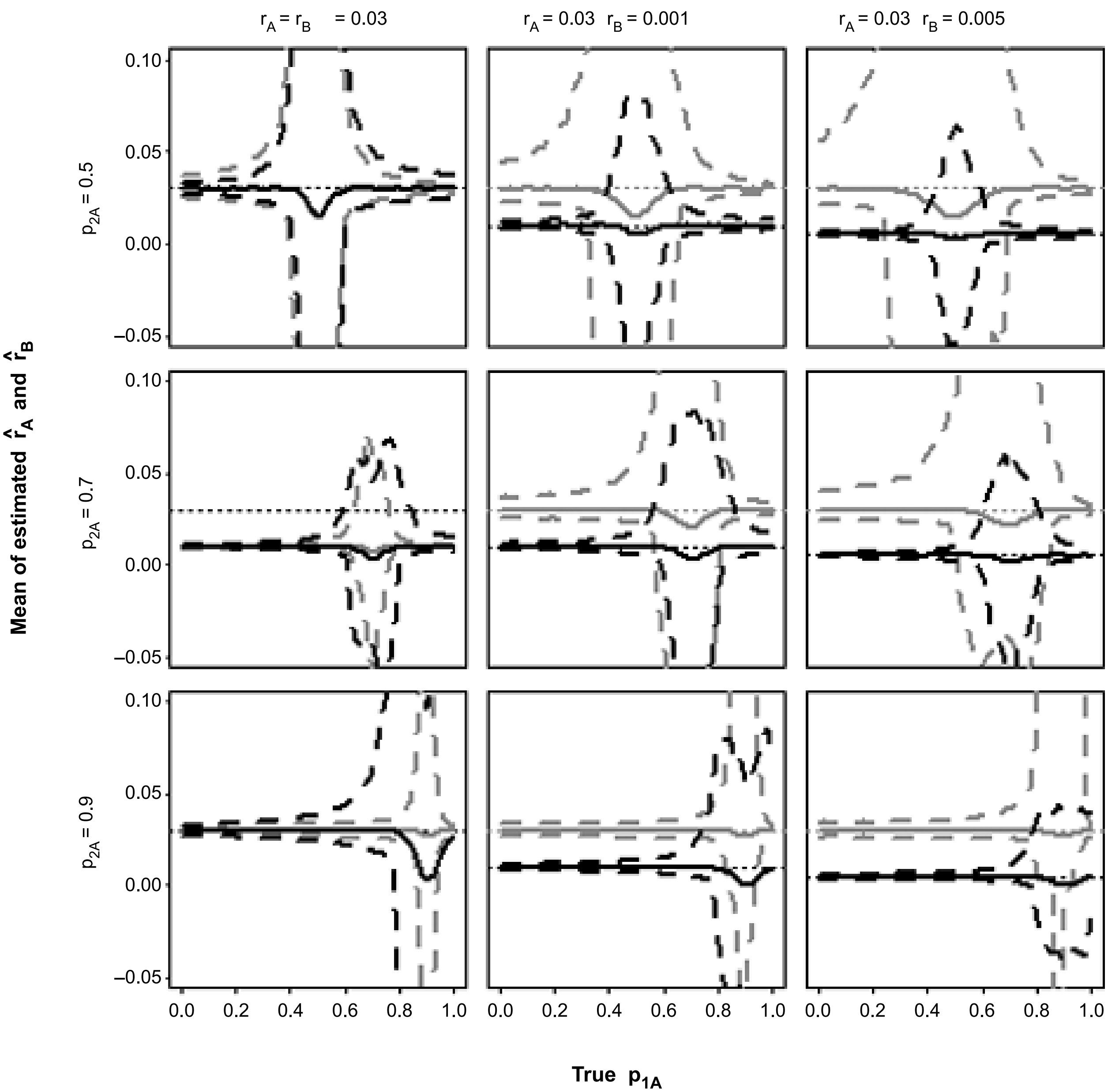

Figure 3. Precision and bias of the estimated re-encounter probabilities $\hat{r}_A$ and $\hat{r}_B$ depending on the difference between true p_{1A} and true p_{2A} and the proportion of true re-encounter probability r_A to r_B. Bold lines, means of 5000 estimated re-encounter probabilities $\hat{r}_A$ and $\hat{r}_B$; broken lines, 0.025 and 0.975 quantiles of these estimates; dotted lines, true values r_A and r_B; grey, destination area A; black, destination area B; true p_{2A} is set to 0.5, 0.7, or 0.9; true p_{1A} varies from 0 to 1 (by step 0.02). Results are shown for three different ratios for re-encounter probabilities. Unbiased estimates lie around horizontal lines at the height of their true values.

Differences in wintering areas between sexes can also be analysed, if it can be assumed that their mortality between ringing and destination areas are similar and their re-encounter probability equal. Such requirements might be met, for example, in some passerines and waders with low dimorphism.

COMMONALITY OF DIVISION COEFFICIENTS AND MULTI-STATE MODELS

The division coefficient can be seen as a synonym for the migration (transition) rate in a multi-state mark–recovery model as proposed by Schwarz (1993) or

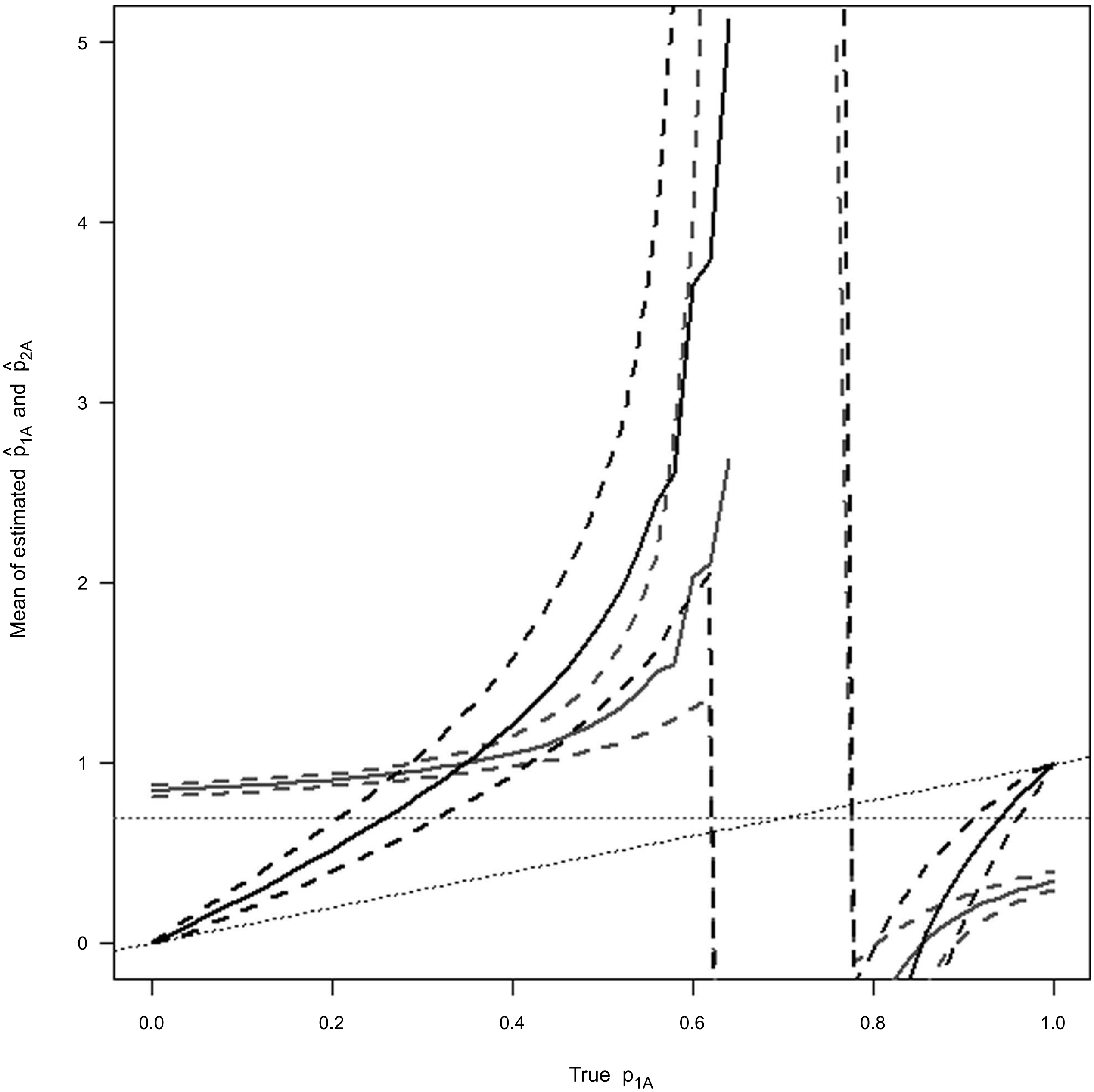

Figure 4. Estimates of division coefficients $\hat{p}_{1A}$ and $\hat{p}_{2A}$ (bold lines) compared with true values p_{1A} and p_{2A} (dotted lines) for simulated data sets for which the assumption of equal re-encounter probability in both bird groups is violated. These data sets were simulated releasing 60 000 virtual birds in each group. Number of re-encounters per group and destination area were simulated using a true division coefficient for group 1 p_{1A} varying from 0 to 1 with step 0.02 and for group 2 p_{2A} = 0.7, and using group dependent re-encounter probabilities (r_1 = 0.03, r_2 = 0.01) instead of area-dependent re-encounter probabilities as for Figs. 2 and 3. Then, estimated division coefficients $\hat{p}_{1A}$ and $\hat{p}_{2A}$ were calculated (thereby assuming equal re-encounter probabilities between the groups).

Thorup & Conn (2009). However, in multi-state models migration rates normally include movements of birds within short time intervals, whereas the division coefficient measures the cumulated movements over a long time period, i.e. bird distribution rather than bird movement. If many short time intervals are included in a multi-state model, survival can be estimated in addition. It is also possible to construct a multi-state model for one long time period instead of many small time intervals, so that the division coefficient equals the migration rate. Then, survival is confounded with re-encounter probability. In such a model, the expected number of re-encounters per group and destination area is modelled as a product: $E(V_{GT}) = N_G\, p_{GT}\, r_T$. For an example with two groups G and two destination areas T we have the following relationships making use of the constraint $p_{GA} + p_{GB} = 1$:

$$\begin{aligned} E(V_{1A}) &= N_1 p_{1A} r_A \\ E(V_{1B}) &= N_1(1-p_{1A}) r_B \\ E(V_{2A}) &= N_2 p_{2A} r_A \\ E(V_{2B}) &= N_2(1-p_{2A}) r_B. \end{aligned} \tag{7}$$

For estimates of the migration rates and re-encounter probabilities we require that these equations hold for the observed instead of the expected values:

$$\begin{aligned} V_{1A} &= N_1 \hat{p}_{1A} \hat{r}_A \\ V_{1B} &= N_1(1-\hat{p}_{1A}) \hat{r}_B \\ V_{2A} &= N_2 \hat{p}_{2A} \hat{r}_A \\ V_{2B} &= N_2(1-\hat{p}_{2A}) \hat{r}_B. \end{aligned} \tag{8}$$

Now, if V_{GT} in Equation system 1 are replaced by Equation system 8, and the system solved for $\hat{x}_T$, we get $\hat{x}_T = \frac{1}{\hat{r}_T}$, which is the interpretation of $\hat{x}_T$ in the division coefficient concept after Kania & Busse (1987). Indeed, it can be shown that the maximum likelihood solution for migration rate and re-encounter probability in the multi-state model is equal to the solution of Equation system 1 proposed by Kania & Busse (1987), if the number of groups and the number of areas is the same and if certain technical assumptions are satisfied (Appendix 1, see also Davidson & Solomon [1974] for a more general discussion about the relation of the method of moments and the method of maximum likelihood). Therefore, the division coefficient proposed by Busse & Kania (1977) is equivalent to the migration rate estimated by a multi-state model in these cases.

BOOTSTRAP CONFIDENCE INTERVALS FOR THE DIVISION COEFFICIENT

Bootstrapping is an appropriate method to assess the sensitivity to random variation of the estimated division coefficient. It allows for receiving uncertainty measurements such as standard errors and confidence intervals (Simon 1997, Carpenter & Bithell 2000). Here we calculate non-parametric bootstrap confidence intervals for the example given in Fig. 1. Random samples with replacement have to be drawn from all ringed birds (pooled for both groups). This is done $K = 5000$ times. For each bootstrap sample, the number of birds per group N^{boot}_{Gk} for k in 1, …, K and the number of re-encounters in each destination area V^{boot}_{GTk} has to be counted, and the estimated division coefficients for both groups $\hat{p}^{boot}_{GTk}$ calculated by solving Equation system 1. From the distribution of $\hat{p}^{boot}_{GTk}$ the 0.025 and 0.975 quantiles give the limits of the 95% confidence intervals. Because, in some cases, estimated division coefficients can become below 0 or above 1, which are meaningless values, such values are set to 0 or 1 respectively. Therefore, the median instead of the mean of $\hat{p}^{boot}_{GTk}$ is used as a bootstrap estimate. The syntax for calculating the bootstrap confidence intervals in R is given in Appendix 2.

The bootstrap estimates of the division coefficients and their 95% confidence intervals for the example given in Fig. 1 were $\hat{p}_{1A} = 0.51$ (0, 0.83) and $\hat{p}_{2A} = 0.20$ (0, 0.39). In this case, the uncertainty of the estimates is relatively high, which is most likely due to the large difference in re-encounter probability (factor 10) between area A and B, combined with a moderate difference in division coefficient between the groups.

DISCUSSION

We showed mathematically that the division coefficient is the maximum likelihood estimate of a multi-state model if applied to one long time period instead of many short time intervals. This suggests that, in both methods, similar requirements have to be met in order to get precise estimates. For getting precise and unbiased estimates, in both methods, a large difference in division coefficient/migration rate between groups and no difference between groups in re-encounter probabilities must be present in the data. The former requirement is more important if differences in re-encounter probabilities between the areas are large. In multi-state models parameters might not be estimable due to the specific structure of the data, even if the model is intrinsically identifiable (Catchpole *et al.* 2001, Brooks *et al.* 2002, Schaub *et al.* 2004, Schaub 2009). In the simulations presented here, we described such data structures for which parameter estimations in the division coefficient method failed. Because of the mathematical equivalency of the division coefficient and the simple multi-state model, parameter estimation in multi-state models will behave similarly in relation to data structure.

We showed that the parameter estimates obtained by the division coefficient method are also the maximum likelihood estimates of a multi-state model if the number of bird groups and the number of re-encounter areas are higher than two, given that these two numbers are equal (Appendix 1). It remains to be investigated whether the two methods are equivalent when the number of bird groups exceeds the number of re-encounter areas. Furthermore, we showed that the precision of the estimated division coefficients is low when their true values are similar between the two bird groups. We do not know how this rule is generalized to a case with more than two bird groups. For such cases it is valuable to conduct simulation studies, as presented here, in order to explore the behaviour of parameter estimation.

The similarity between the division coefficient method and the multi-state model leads to the question as to when to choose which method. Multi-state models are used to describe the dynamics of movements. They allow the investigation of how many birds move between different areas per time interval. In contrast, the division coefficient is a description of a (static) bird distribution and thus can be a tool for describing migratory connectivity as defined by Webster *et al.* (2002). Multi-state models are more flexible. They allow the estimation of migration rates as well as survival rates over several time periods, time dependency of the parameters can be explored and covariates included in the model. However, when using a multi-state model ornithologists need to be familiar with the theory in statistical modelling, and they need to know how to use specific software (e.g., MARK). In contrast, the division coefficient method is easier to understand and apply because only a simple equation system needs to be solved. It would be valuable to compare the performance of both methods if applied to real data examples.

Here, we showed that the division coefficient method with the bootstrap confidence intervals can be used instead of a multi-state model if the bird distribution between destination areas (e.g. migratory connectivity) alone is of interest.

An R-function to calculate the division coefficient with the bootstrap interval is provided at http://www.vogelwarte.ch/home.php?lang=e&cap=projekte&subcap=vogelzug.

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APPENDIX 1

Mathematical evidence that the maximum likelihood solution for the migration rates and re-encounter probabilities in a multi-state model is equal to the solution of the division coefficient concept if the number of groups equals the number of destination areas.

We determine the maximum likelihood estimates for the parameters of a multi-state model with n groups and n destination areas, where

$$\left(V_{G1}, V_{G2}, \dots, V_{Gn}, N_G - \sum_{T=1}^{n} V_{GT}\right)$$

are multinomially distributed with N_G observations (i.e. number of ringed and released birds per group) and probabilities

$$\left(p_{G1}r_1, p_{G2}r_2, \dots, p_{Gn}r_n, 1 - \sum_{T=1}^{n} p_{GT}r_T\right)$$

within each group $G \in 1,\dots, n$ (i.e. the probabilities that a bird of group G is migrating to and is recovered in destination areas $T = 1,\dots,n$). The counts for different groups are assumed to be independent.

Our aim is to show that these maximum likelihood estimates are equal to the estimates resulting from the division coefficient method. We assume that all counts V_{GT} are positive and also that $N_G - \sum_{T=1}^{n} V_{GT} > 0$ (i.e. from every group, some birds are not recovered). We also have to assume that the maximum likelihood estimates satisfy $\hat{p}_{GT}\hat{r}_T > 0$.

We write $q_{GT} = p_{GT}r_T$ for the multinomial probabilities in the above model. The likelihood function for the multi-state model is

$$L = \prod_{G=1}^{n} L_G = \prod_{G=1}^{n} \left[\frac{N_{G!}}{V_{G1}! \cdot V_{G2}! \cdot \ldots \cdot V_{Gn}! \cdot (N_G - \sum_{T=1}^{n} V_{GT})!} \left(\prod_{T=1}^{n} q_{GT}^{V_{GT}}\right) \left(1 - \sum_{T=1}^{n} q_{GT}\right)^{N_G - \sum_{T=1}^{n} V_{GT}} \right].$$

If we are able to find values $\hat{q}_{GT} = \hat{p}_{GT}\hat{r}_T$ that maximize the likelihood L_G for each group separately, then these values will also maximize the full likelihood L. In order to maximize L_G, we consider its logarithm,

$$\lambda_G = \log\left(\frac{N_G!}{V_{G1}! \cdot V_{G2}! \cdot \ldots \cdot V_{Gn}! \cdot (N_G - \sum_{T=1}^{n} V_{GT})!}\right) + \sum_{T=1}^{n} V_{GT} \log q_{GT} + \left(N_G - \sum_{T=1}^{n} V_{GT}\right) \log\left(1 - \sum_{T=1}^{n} q_{GT}\right)$$

and set all its partial derivatives to zero:

$$\frac{\partial \lambda_G}{\partial q_{GT}} = \frac{V_{GT}}{q_{GT}} - \frac{N_G - \sum_{T'=1}^{n} V_{GT'}}{1 - \sum_{T'=1}^{n} q_{GT'}} \overset{!}{=} 0, \quad \forall T \in \{1,\dots,n\}.$$

(Generally, these are only necessary conditions for a maximum. However, since the matrix of the second partial derivatives is negative, as long as all observed counts are positive, these equations do yield a maximum in our case.)

Therefore, the maximum likelihood estimates $\hat{q}_{GT}$ are given by

$$\begin{cases} \dfrac{V_{G1}}{\hat{q}_{G1}} - \dfrac{N_G - \sum_{T'=1}^{n} V_{GT'}}{1 - \sum_{T'=1}^{n} \hat{q}_{GT'}} = 0, \\ \dfrac{V_{G1}}{\hat{q}_{G1}} = \dfrac{V_{GT}}{\hat{q}_{GT}}, \quad \forall T \in \{2,\dots,n\}. \end{cases}$$

Assuming that all $\hat{q}_{GT} \neq 0$ and that $1 - \sum_{T=1}^{n} \hat{q}_{GT} \neq 0$, we obtain

$$\begin{cases} V_{G1}\left(1 - \sum_{T'=1}^{n} \dfrac{V_{GT'}\hat{q}_{G1}}{V_{G1}}\right) = \hat{q}_{G1}\left(N_G - \sum_{T'=1}^{n} V_{GT'}\right), \\ \hat{q}_{GT} = \dfrac{V_{GT}\hat{q}_{G1}}{V_{G1}}, \quad \forall T \in \{2,\dots,n\}, \end{cases}$$

which simplifies to

$$\begin{cases} \hat{q}_{G1} = \dfrac{V_{G1}}{N_G}, \\ \hat{q}_{GT} = \dfrac{V_{GT}}{N_G}, \quad \forall T \in \{2,\dots,n\}. \end{cases}$$

These conditions for the maximum likelihood parameter estimates in every group $G \in 1,\dots, n$ are fulfilled by the estimates resulting from the division coefficient method, since for these estimators, according to Equations 3 and 4,

$$\hat{p}_{GT}\hat{r}_T = \frac{V_{GT}\hat{x}_T}{N_G} \cdot \frac{1}{\hat{x}_T} = \frac{V_{GT}}{N_G}, \quad \forall G \in \{1,\dots,n\}, T \in \{1,\dots,n\}.$$

Therefore, the division coefficient estimates maximize the likelihood L of the multi-state model.

APPENDIX 2

Example R-syntax for calculating bootstrap confidence intervals of the division coefficient for the data given in Kania & Busse (1987) and Fig. 1 in this study. An R-function to calculate the division coefficient and its bootstrap interval for cases with more groups than destination areas is provided at http://www.vogelwarte.ch/home.php?lang=e&cap=projekte&subcap=vogelzug.

```
##########################################################################
# R-Code for calculating bootstrap confidence intervals
# of the division coefficient for the case with two bird groups (1, 2) and
# two re-encounter areas (A, B)
#
# R-Code developed for R 2.6.1, March 2008
# The software R can be downloaded and installed from www.r-project.org
#
# Insert number of ringed and recovered birds in the first three
# lines of the code. Then, copy and paste the whole code into
# the R-console. The procedure will need several minutes.
##########################################################################


# Insert the observed number of ringed and recovered birds per group here:
N<-c(10000, 15000)                  # number of ringed birds of group 1 and 2
VA<-c(100, 60)                      # number of birds recovered in A per group 1
                                      and 2
VB<-c(10, 24)                       # number of birds recovered in B per group 1
                                      and 2


nx<-matrix(c(VA,VB), ncol=2)
x.hat.obs<-solve(nx, N)
1/x.hat                             # estimated re-encounter rates in A and B
div.coef.hat.obs<-x.hat.obs[1]*VA/N # division coefficients p̂GA
div.coef.hat.obs                    # print observed division coefficients


# create data with one row for each individual
dat<-data.frame(group=c(rep(1, N[1]), rep(2, N[2])),
rec=c(rep(0, N[1]-VA[1]-VB[1]), rep("A", VA[1]), rep("B", VB[1]), rep(0, N[2]-VA[2]-VB[2]),
rep("A", VA[2]), rep("B", VB[2])))

# start bootstrapping
K<-5000                             # number of replicates
div.coef.hat<-data.frame(p1=numeric(K), p2=numeric(K))
for(k in 1:R){
        dat.boot<-dat[sample(1:dim(dat)[1], replace=TRUE),]     # sample
        N.boot<-table(dat.boot$group)                           # count N^boot_Gk
        VA.boot<-table(dat.boot$group[dat.boot$rec=="A"])       # count V^boot_GAk
        VB.boot<-table(dat.boot$group[dat.boot$rec=="B"])       # count V^boot_GBk
```

```
        nx<-matrix(c(VA.boot,VB.boot), ncol=2)
        x.hat<-solve(nx, N.boot)                                  # solve equation system
        div.coef.hat[k,]<-x.hat[1]*VA.boot/N.boot # division coef.    p̂^boot_GAk
        }
div.coef.hat$p1[div.coef$p1<0]<-0                                 # set values below 0 to 0
div.coef.hat$p2[div.coef$p2<0]<-0
div.coef.hat$p1[div.coef$p1>1]<-1                                 # set values above 1 to 1
div.coef.hat$p2[div.coef$p2>1]<-1
median(div.coef.hat$p1)                                           # bootstrap estimates of p_1A
median(div.coef.hat$p2)                                           # bootstrap estimates of p_2A
quantile(div.coef.hat$p1, c(0.025, 0.975)) # 95% confidence interval for p_1A
quantile(div.coef.hat$p2, c(0.025, 0.975)) # 95% confidence interval for p_2A
```