

Testing sexual segregation and aggregation: old ways are best

Christophe Bonenfant, Jean-Michel Gaillard, Anne Loison, Manuela Royer, Daniel Chessel

▶ **To cite this version:**

Christophe Bonenfant, Jean-Michel Gaillard, Anne Loison, Manuela Royer, Daniel Chessel. Testing sexual segregation and aggregation: old ways are best. Ecology, 2007, 88 (12), pp.3202-3208. 10.1890/07-0129.1 . hal-01107529

HAL Id: hal-01107529
https://hal.science/hal-01107529

Submitted on 17 Feb 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

TESTING SEXUAL SEGREGATION AND AGGREGATION: OLD WAYS ARE BEST

Christophe Bonenfant[1], Jean-Michel Gaillard, Stéphane Dray, Anne Loison, Manuela Royer & Daniel Chessel

April 28, 2007

Université de Lyon ; Université Lyon 1 ; CNRS ; UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, 43 boulevard du 11 novembre 1918, Villeurbanne F-69622, France.

[1] E-mail: bonenfan@biomserv.univ-lyon1.fr

Abstract. The study of sexual segregation has received increasing attention over the last two decades. Several hypotheses have been proposed to explain the existence of sexual segregation , such as the "predation risk hypothesis", the "forage selection hypothesis" and the "activity budget hypothesis". Testing which hypothesis drives sexual segregation is hampered, however, by the lack of consensus regarding a formal measurement of sexual segregation. By using a derivation of the well-known Chi-square (called SSAS) instead of existent segregation coefficients, we offer a reliable way to test for temporal variation in the occurrence of sexual segregation and aggregation, even in cases where a large proportion

of animals are observed alone. A randomization procedure provides a test for the null hypothesis of independence of the distributions of males and females among the groups. The usefulness of SSAS in the study of sexual segregation is demonstrated with three case studies on ungulate populations belonging to species with contrasting life histories and annual grouping patterns (isard, red deer and roe deer). The existent segregation coefficients were unreliable since for a given value, sexual segregation could or could not occur. Similarly, the existent segregation coefficients performed badly when males and females aggregated. The new SSAS was not prone to such limitations and allowed clear conclusions regarding whether males and females segregate, aggregate or simply mix at random applicable to all species.

Key-words: Capreolus capreolus*;* Cervus elaphus*; Chi-square; Isard; Red deer; Roe deer;* Rupicapra pyrenaica*; Sexual aggregation; Segregation coefficient; Sexual segregation.*

Introduction

The study of sexual segregation (Darwin 1859, 1871), the separation of males and females by habitat, spatially or socially outside of the breeding season (MacCullough et al. 1989), has received increasing attention over the last 2 decades (Bowyer 2004). This phenomenon appears to be common among a large range of animal species (Bleich et al. 1997, Ruckstuhl and Neuhaus 2005). Several non-exclusive hypotheses have been proposed to explain sexual segregation (Bon and Campan 1996, Bowyer 2004, Ruckstuhl and Kokko 2002). Among them the "predation risk hypothesis" (Bleich et al. 1997, Bowyer 1984, Miquelle et al. 1992), the "forage selection hypothesis" (Clutton-Brock et al. 1987, Staines et al. 1982) and the "activity budget hypothesis" (Ruckstuhl 1998, Ruckstuhl and Neuhaus 2000) are the most frequently mentioned

(Bowyer 2004). However, the degree to which any one of the hypothesis can account for most observed situations is still unclear (Mooring and Rominger 2004 vs. Neuhaus and Ruckstuhl 2004; Ruckstuhl and Neuhaus 2002 vs. Yearsley and Pérez-Barbéria 2005).

Confusion about sexual segregation terminology (Barboza and Bowyer 2000, Bowyer 2004, Bowyer et al. 1996, Main et al. 1996) and a lack of a general measurement of sexual segregation hinders our ability to uncover the mechanisms driving the evolution of sexual segregation. For example, while Conradt (1998) reviewed 3 potential methods to quantify sexual segregation, additional measurements could have been used such as Edwards' distance (Edwards 1971), the Overlap index ('D2', Manly 2005) or Nei's distance (Nei 1972). The use of so many indices based on different metrics has prevented reliable inter-specific or inter-population comparisons despite the potential pivotal role of such comparisons to our broader understanding of the evolution of sexual segregation (Mysterud 2000).

In an attempt to develop a formal measure of segregation, Conradt (1998) proposed that the deviation of the observed group composition by sex from a random association of animals is an objective definition of sexual segregation. The resulting "segregation coefficient" (SC) provided a measure supposedly independent of stochastic variations such as sex ratio, group size, or the number of observations. It should also allow one to differentiate the relative importance of social, habitat and spatial segregation (Bon 1991, Conradt 1998). Despite its interesting properties, the segregation coefficient has seldom been used (< 10 reported uses out of about 100 papers published per year since 2000) likely because of its mathematical formulation and its lack of software implementation. However, the segregation coefficient (Conradt 1998) has recently been criticised as being unnecessarily conservative because it excludes "groups" composed of single animals (Bowyer 2004), which could be particularly important in some species. Thus, the segregation coefficient is unlikely to quantify adequately the annual variations in grouping patterns in slightly gregarious species.

In addition, the segregation coefficient cannot quantify the degree of aggregation in the same way as it does for the degree of sexual segregation (Conradt 1998, 1999). Consequently, the segregation coefficient may not be as generally applicable as once thought so that its use is still controversial.

Here we call for the use of the classical Chi-square statistic which can account for these problems and reliably test how sexual segregation and aggregation change over time, even when a large proportion of animals are solitary. Furthermore, we illustrate the usefulness of the Chi-square statistic and reliably determine whether or not sexual segregation and aggregation occurs in 3 case studies of ungulate populations with contrasting seasonal grouping patterns. We suggest that coming with a measure of sexual segregation may actually be unachievable and that tests for segregation and aggregation should be preferred.

Developing the SSAS

The existing segregation coefficients

Conradt (1998)'s index can be summarized as follows. Considering p_0 (the proportion of males in a group), p_1 (the proportion of females in a group) and p (the average sex ratio), the segregation coefficient should take on values close to 0 when males and females associate at random (all groups will tend to have p_0 nearly equal to p), and reaches a maximum of 1 where sexual segregation is complete (all groups will have p_0 equal to 0 or 1 which are at the maximum distance from p). These parameters correspond to observational data of males and females in each group in sexual segregation studies. The data include k groups with X_i males and Y_i females in the i-th group that can be organised as a 2 by k contingency table. According to Conradt (1998), the original formulation of the SC is:

$$SC = 1 - \frac{N}{XY} \sum_{i=1}^{k} \frac{X_i Y_i}{N_i - 1}$$

where N_i is the group size of the i-th group ($N_i = X_i + Y_i$), X is the total number of males sampled; Y is the total number of females sampled; N is the sum of males and females sampled. Three limitations arise from the assumptions on which SC relies. First, SC is not defined for single animals ($N_i = 1$) because they are thought to segregate from their own sex and thus contribute no information about sexual segregation (Conradt 1998). However, this restriction may miss some obvious cases of sexual segregation. For instance, in the following 5 groups composed of 1, 1, 1, 1, 1 males and 0, 0, 0, 0, 25 females sexual segregation obviously occurs while the SC cannot be calculated. Second, SC can be used only to investigate sexual segregation against random association and aggregation per se is not dealt with. Therefore, SC values tend to be < 0, which prevent using a modified formula suggested as more appropriate (Conradt 1999). Finally, SC has no test against random association.

Linking the segregation coefficient with the SSAS

Testing the occurrence of sexual segregation or aggregation may be solved by considering the data as a standard contingency table and using the well-known Chi-square statistic (Pearson 1900). Indeed, we can easily demonstrate that SCs are closely linked to the Chi-square of the contingency table divided by N (SSAS: Sexual Segregation and Aggregation Statistic, Appendix 1). Using the same notation as for equation 1, this quantity equates to:

$$SSAS = \frac{1}{N}\chi^2 = 1 - \frac{N}{XY} \sum_{i=1}^{k} \frac{X_i Y_i}{N_i}.$$

Thus, by a minor modification of the SCs towards the SSAS, one provides a general

test for the segregation and aggregation patterns observed in natural population, even when dealing with solitary animals. The SSAS being linked with Cramér's V, one of the most popular measures of association between 2 qualitative variables, SASS varies between 0 and 1, regardless of the size of contingency tables (Agresti 1990). As developed below, the major strength of using the SSAS is its ability to test the null hypothesis of a random association between sexes against two alternatives, segregation or aggregation. The expectancy of SSAS is $(k-1)/(N-1)$ (Electronic Appendix 1) and so is inversely related to the mean group size. Being derived from the χ^2, SASS provides an estimate of the distance between the observed and the expected distributions of males and females under the null hypothesis for a given number of groups (k) and animals (N). Consequently, *segregation* is defined as a group by sex composition which is too far from the one obtained under the null hypothesis and *aggregation* as a group by sex composition which is too close to the one obtained under the null hypothesis. Biologically speaking, segregation occurs when the sex ratio of each group is too different from the population sex-ratio (e.g., with many unisex groups for instance). Conversely, aggregation occurs when each group has a sex ratio almost equal to the population sex-ratio.

Testing the significance of segregation or aggregation

The classical χ^2 testing procedure would be appropriate for SSAS if group size were large. However, small groups are common in sexual segregation studies. In such cases, a randomization procedure can be used to test the null hypothesis of independence of the distributions of males and females among groups.

We recommend the following four steps procedure to test for sexual segregation and aggregation: (1) permute data to obtain a contingency table with the same row and column totals as the original contingency table (Patefield 1981); (2) compute the SSAS statistic for the permuted contingency table; (3) repeat steps (1) and (2)

a large number of times (e.g. 999 times) to build a distribution of SSAS under the hypothesis of independence; (4) compare the observed statistic to the distribution obtained by permutation and take the appropriate statistical decision (Fig. 1a-c).

The fourth step differs depending on the alternative hypothesis. If the alternative hypothesis is sexual segregation, then using a significance level equals to α, a P-value is estimated as: (number of random values equal to or larger than the observed one + 1)/(number of permutations + 1). The null hypothesis is rejected if the P-value is less than α. If the alternative hypothesis is sexual aggregation the P-value is estimated as: (number of random values equal to or less than the observed one + 1)/(number of permutations + 1). Again, the null hypothesis is rejected if the P-value is less than the significance level α. Note also that a $(1-\alpha)$ confidence interval can be computed and is bound by the (α)-th and $(1-\alpha)$-th quantile of the permutational distribution (Fig. 1b-d).

When multiple comparison tests are made simultaneously, a Bonferroni correction (the simplest and most conservative approach) on α is needed to perform an overall test at the critical value of α. When groups are composed of solitary individuals only, all permuted tables would be equivalent (owning to the constraint that the sum of rows and columns are preserved). Here, the testing procedure would not fail but the P-value would equal 1 exactly meaning that no segregation occurs. In some species, the assumption of independent animal movements among groups (Electronic Appendix 1) may not be fulfilled (see also Conradt 1998, p. 222). We suggest taking the group of associated animals instead of individual as the sampling unit.

Material

The biological models

Isard (*Rupicapra pyrenaica* Bonaparte), red deer (*Cervus elaphus* L.), and roe deer (*Capreolus capreolus* L.) have contrasting biology and behaviour (Andersen and Linnell 1998, Clutton-Brock et al. 1982). Red deer is a highly dimorphic species with marked segregation of the sexes. At our study site, the dressed body mass of male red deer was 30.4% larger than that of females (respectively 80.4 kg and 59.7 kg, Bonenfant et al. 2002). A recent comparison of two red deer populations (including this population) with different timing of breeding suggested that both the predation risk and the activity budget hypotheses could explain segregation at different times of the year (Bonenfant et al. 2004). Unlike red deer, roe deer are more solitary, forming small groups only during winter (Bideau et al. 1983). Male roe deer were 7.2% larger than females in our study (average live body mass of 26.1 kg and 24.3 kg). Although very few studies have been performed on roe deer sexual segregation (but see Mysterud 1999), we expected only a limited segregation because of the slight dimorphism in size (Andersen and Linnell 1998). The isard is a mountain ungulate, whose sexual size dimorphism is intermediate between red and roe deer (Loison et al. 1999). Despite its rather small sexual size dimorphism (average live body mass of 24.7 kg for females and 25.8 kg for males, i.e. a 6.7% dimorphism), social and habitat segregation of male and female isard have previously been documented in the Alps (Shank 1985).

The data

The data set on the 3 ungulate species were collected continuously from January to December by fieldworkers from the Office National de la Chasse et de la Faune Sauvage (ONCFS) in France (all available at: `http://pbil.univ-lyon1.fr/R/donnees/`).

The red deer dataset includes 677 group observations made in the La Petite Pierre National Reserve (Bonenfant et al. 2002) between 1980 and 1999. The roe deer dataset includes 1214 groups observed in the Trois-Fontaines "Territoire d'Étude et d'Experimentation" (Gaillard et al. 1993) in 1981 and 1982. The isard dataset, included annual observations of isard in the Bazes, yielding a total of 265 recorded groups (Loison et al. 2002, for details) from 1998 to 2000. For the 3 study sites, group composition was collected daily either on foot or by car. Sex- and age-class of each individual (young of the year, yearling or adult) was recorded. For a given month, group composition of all years were pooled as we currently have no evidence for annual changes in sexual segregation patterns (Bonenfant et al. 2004).

Results

When conducting the analyses on red deer using SSAS for each month, we observed conspicuous temporal variation in sexual segregation, with significant segregation occurring only during 3 months (April, May and June) and sexual aggregation occurring during 3 months in winter (November, January and February, Fig. 2c). The SSAS testing procedure provided us with a more informative picture of the temporal variation in sexual segregation than the SC (Fig. 2d).

Roe deer males and females did not segregate during any month (all SSAS tests against segregation have $P > 0.05$). From the tests of SSAS against aggregation, roe deer in July and December were found to show significant aggregation of the sexes (Fig. 2e). A high frequency of single animal groups (78%) was found for roe deer (average group size: 1.27 ± 0.60). In eleven out of twelve months, the negative values of the SC suggested that male and females roe deer aggregate (Fig. 2f). However, this result is incorrect as neither segregation nor aggregation could be detected except in two months when testing with the SSAS.

In spite of the gregariousness nature of isard (average group size: 7.84 ± 7.32),

aggregation of males and females did not occur in any month and sexual segregation was high and significant all year (all SSAS tests have $P < 0.05$, Fig. 2a). Solitary individuals were not observed in isard. Compared to SC (Fig. 2b), only the SSAS provided a clear-cut conclusion that sexual segregation in isard was significant all year-round.

Discussion

Testing or measuring sexual segregation?

The use of SSAS does not lead to a measure of segregation per se, but to a test of segregation and aggregation compared to a random association of males and females. Defining a measure of dependence for categorical data is a general problem in statistics and "there may be no general solution to the problem of finding such a measure" (Lancaster 1969, p. 239). Like the χ^2, SSAS values cannot be used as a measure of the strength of sexual segregation (Agresti 1990). Only the test of SSAS is relevant and should be used as a decision rule (random association vs. segregation or aggregation). Comparing SSAS values is meaningless unless one estimates the confidence limits (CI) around the observed values to account for the sampling variance. However, obtaining these confidence limits assumes that the distributional properties of SSAS are known under the null and alternative hypotheses. Under H_0, $N\times$ SSAS would follow a χ^2 distribution if both the sample sizes are large and k (the number of groups) is held constant. Under H_1, $N\times$ SSAS would follow a non-centered χ^2 distribution at two conditions: (1) sample sizes are large, and (2) an assumption detailed in Electronic Appendix 1 is met (Theorem 6). This second assumption cannot be verified in practise because "group" is not a fixed label and it varies in time (Electronic Appendix 1, Theorem 8). This prevents estimating CI around SSAS values. Consequently, one cannot conclude that segregation is stronger or weaker in two different species or

among months for a given species, by simply and directly comparing SSAS (e.g., for isard and roe deer). Nevertheless, we demonstrate below that this limitation also holds for the SC.

Several mathematical problems undermine the validity of the segregation coefficients (SC) and here we list some of the most significant. Although presented as a measure of sexual segregation (Conradt 1998), the SC is not. The expected value of SC is not 0 but is $-1/(N-1)$ (Electronic Appendix 1, Corollary 7) in Conradt (1998)'s formulation. Similarly, using the corrected formula (Conradt 1999), the expected value of the SC still does not equal 0 and is ill-defined under H_0 (the sum under the square root may take negative values: Electronic Appendix 1, Corollary 7). Hence for both SC formulations, 0 cannot be taken as a baseline for a random association of the sexes. Besides, contrary to SASS which is based on the difference between the observed and the expected distribution of males and females among groups under H_0, the SC formulation does not call for the expected values of the contingency table. Consequently, a test of SC does not warrant a test against a random association of the sexes in all cases (even with a randomization procedure). Lastly, as shown for the SSAS values, comparing two values of SCs does not provide any information about a possible difference of sexual segregation. In addition, excluding solitary animals can yield erroneous results, such as concluding wrongly to a spurious aggregation pattern, as we observed for roe deer (Figs. 2e–f). Clearly, both SC formulations cannot reliably handle aggregation patterns or be applied to only slightly gregarious species.

Even though SSAS and SC values share close mathematical formulations, their use to assess the biological patterns profoundly differs. Consequently, we call for a test based on SSAS values. The biological knowledge about sexual segregation and aggregation is better achieved with the SSAS testing procedure than with the SC. Most of time, no firm conclusion can be reached from the SC since it cannot set apart a random association of the sexes from a true segregation – aggregation process. For example, the SC value in July for the red deer is 0.20 (Fig. 2d), from

which we cannot conclude whether sexual segregation occurs or not. For isard (Fig. 2b), approximately the same SC value (0.20) is found in June. Following Conradt (1998)'s approach, sexual segregation should be similar in both species (same value of SC: 0.2). However, sexual segregation occurs only in isard, but does not in red deer as the test of SSAS showed (Figs. 2a–c). Such discrepancies between the interpretation of SC and SSAS emphasise the importance of testing for group patterns rather than measuring any value.

Biological interpretation of SSAS

Using SSAS, we uncovered three dramatically different processes on three contrasting species. For isard, gregariousness was found all year-round and associated with a year-persistent sexual segregation. Such a pattern is consistent and generally described in other mountain ungulates (bighorn sheep, *Ovis canadensis* Shaw, and ibex, *Capra ibex* L., see Ruckstuhl and Neuhaus 2000). Gregariousness varied according to the season for red deer, with significant segregation during 3 months, and significant aggregation during 3 months, supporting the anti-predator tactic as the segregation only occurred during the calving season (Bonenfant et al. 2004). We confirmed the solitary tendency of roe deer, except during winter when they form larger groups (Bideau et al. 1983, Hewison et al. 1998). Association between male and female roe deer was mostly random, except during the mating period (July, see Bramley 1970). Hence, the three species displayed three different and contrasting grouping patterns that an average value would have not revealed.

Comparing SSAS values for a given species or among species is tempting (e.g., Bonenfant et al. 2004, Loe et al. 2006, Coulson et al. 2006), but is not recommended. Among-species comparisons with the SSAS testing procedure are possible however by building a typology of the grouping patterns. Such a classification is needed because of the strong temporal structure in group composition and group size (Bowyer 2004),

and because the underlying process of sexual segregation differs according to the species' social structure (e.g., occurrence of matrilineal groups). Using SSAS, one can distinguish sexually segregated species presenting a full segregation year-round (like the isard) from species with seasonal segregation (like the red deer).

Conclusion

The proposed SSAS approach offers biologists a general solution to the problem of how to detect both segregation and aggregation. This approach is applicable to all species at any time of their life cycle, and was already provided more than 100 years ago. We emphasise that SSAS comes with a ready-to-use function (Electronic appendix 2) to be run in the free software R (R Development Core Team 2006). The current SSAS testing procedure assesses the occurrence of segregation – aggregation i.e., it does not differentiate among the habitat and the social components of sexual segregation. As SSAS is based on the χ^2 theory, the decomposition of SSAS can be computed with adequate statistical tools like Chi-square decompositions, log-linear models (Agresti 1990) or correspondence analyses where environmental descriptors can be entered as explanatory variables. Consequently, all these methods will allow one to separate social from habitat segregation or to investigate the effects of sex ratio or density on animal grouping behaviour.

Acknowledgments

We warmly thank everyone involved in countless hours of data collection. We greatly appreciated the contribution made by François Klein and Daniel Maillard (ONCFS) for permitting part of their data to fall into the public domain. We are indebted to Marco Festa-Bianchet, Terry Bowyer, John Lesku, Jos Milner, Atle Mysterud, Jorge A. Navarro Alberto, Kathreen Ruckstuhl and two anonymous referees for constructive comments on previous drafts of the manuscript. The Centre National de la Recherche

Scientifique (CNRS), the University of Lyon and the Office National de la Chasse et de la Faune Sauvage (ONCFS) provided financial support of this work.

Literature Cited

Agresti, A., 1990. Categorical data analyses. Wiley – Interscience Publication, New-York.

Andersen, R. and J. D. C. Linnell, 1998. Ecological correlates of mortality of roe deer fawns in a predator-free environment. Canadian Journal of Zoology **76**:1217–1225.

Barboza, P. S. and T. R. Bowyer, 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. Journal of Mammalogy **81**:473–489.

Bideau, E., J. Vincent, and F. Maire, 1983. Evolution saisonnière de la taille de groupe chez le chevreuil en milieu forestier. Revue d'Ecologie – La Terre et la Vie **37**:161–169.

Bleich, V. C., T. R. Bowyer, and J. D. Wehausen, 1997. Sexual segregation in mountain sheep: Resources or predation? Wildlife Monographs **134**:3–50.

Bon, R., 1991. Social and spatial segregation of males and females in polygamous ungulates: proximate factors. In F. Spitz, G. Janeau, G. Gonzales, and S. Aulagnier, editors, *Ongulés/Ungulates 1991. Proceedings of the International Symposium Ongulés/Ungulates 1991*, pages 195–198, Paris. S. F. E. M. P. – I. R. G. M.

Bon, R. and R. Campan, 1996. Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach. Behavioural Processes **38**:131–154.

Bonenfant, C., J.-M. Gaillard, F. Klein, and A. Loison, 2002. Sex- and age-dependent

effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. Ecography **25**:446–458.

Bonenfant, C., L. E. Loe, A. Mysterud, R. Langvatn, N. C. Stenseth, J. M. Gaillard, and F. Klein, 2004. Multiple causes of sexual segregation in European red deer: enlightenments from varying breeding phenology at high and low latitude. Proceedings of the Royal Society of London Series B **271**:883–892.

Bowyer, R. T., 2004. Sexual segregation in ruminants: Definitions, hypotheses, and implications for conservation and management. Journal of Mammalogy **85**:1039–1052.

Bowyer, T. R., 1984. Sexual segregation in southern mule deer. Journal of Mammalogy **65**:410–417.

Bowyer, T. R., J. G. Kie, and V. Van Ballenberghe, 1996. Sexual segregation in black-tailed deer: effect of scale. Journal of Wildlife Management **60**:10–17.

Bramley, P., 1970. Territoriality and reproductive behaviour of roe deer. Journal of Reproduction and Fertility **S11**:43–70.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon, 1982. Red deer : behavior and ecology of two sexes. University of Chicago Press, Chicago.

Clutton-Brock, T. H., G. R. Iason, and F. E. Guinness, 1987. Sexual segregation and density-related changes in habitat use in male and female Red deer (*Cervus elaphus*). Journal of Zoology **211**:275–289.

Conradt, L., 1998. Measuring the degree of sexual segregation in group-living animals. Journal of Animal Ecology **67**:217–226.

Conradt, L., 1999. Social segregation is not a consequence of habitat segregation in red deer and feral Soay sheep. Animal Behaviour **57**:1151–1157.

Coulson, G., A. MacFarlane, S. Parsons, and J. Cutter, 2006. Evolution of sexual segregation in mammalian herbivores: kangaroos as a marsupial models. Autralian Journal of Zoology **54**:217–224.

Darwin, C., 1859. On the origin of species by means of natural selection or, the preservation of favoured races in the struggle for life. John Murray, London.

Darwin, C., 1871. The descent of man and selection in relation to sex. John Murray, London.

Edwards, A., 1971. Distance between populations on the basis of gene frequencies. Biometrics **27**:873–881.

Gaillard, J.-M., D. Delorme, J.-M. Boutin, G. van Laere, B. Boisaubert, and R. Pradel, 1993. Roe deer survival patterns: a comparative analysis of contrasting population. Journal of Animal Ecology **62**:778–791.

Hewison, A., J. Vincent, and D. Reby, 1998. The European roe deer: The biology of success, chapter Social organisation of European roe deer, pages 189–219. Scandinavian University Press, Oslo.

Lancaster, H. O., 1969. The Chi-squared distribution. Wiley Publications in Statistics, New York.

Loe, L., R. Irvine, C. Bonenfant, A. Stien, R. Langvatn, S. Albon, A. Mysterud, and N. Stenseth, 2006. Testing five hypotheses of sexual segregation in an arctic ungulate. Journal of Animal Ecology **75**:485–496.

Loison, A., J. M. Gaillard, C. Pélabon, and N. G. Yoccoz, 1999. What factors shape sexual size dimorphism in ungulates? Evolutionary Ecology Research **1**:611–633.

Loison, A., C. Toïgo, J. Appolinaire, and J. Michallet, 2002. Demographic processes

in colonizing populations of isard (*Rupicapra pyrenaica*) and ibex (*Capra ibex*). Journal of Zoology **256**:199–205.

MacCullough, D., D. Hirth, and S. Newhouse, 1989. Resource partitionning between sexes in white-tailed deer. Journal of Wildlife Management **53**:277–283.

Main, M. B., F. W. Weckerly, and V. C. Bleich, 1996. Sexual segregation in ungulates: new directions for research. Journal of Mammalogy **77**:449–461.

Manly, B., 2005. Multivariate statistical methods: A primer. Champan & Hall, Boca Raton.

Miquelle, D. G., J. M. Peek, and V. van Ballenberghe, 1992. Sexual segregation in Alaskan moose. Wildlife Monographs **122**:1–57.

Mooring, M. and E. Rominger, 2004. Is the activity budget hypothesis the holy grail of sexual segregation? Behaviour **141**:521–530.

Mysterud, A., 1999. Seasonal migration pattern and home range of roe deer (capreolus capreolus) in an altitudinal gradient in southern norway. Journal of Zoology **247**:479–486.

Mysterud, A., 2000. Diet overlap among ruminants in Fennoscandia. Oecologia **124**:130–137.

Nei, M., 1972. Genetic distance between populations. American Naturalist **106**:283–.

Neuhaus, P. and K. Ruckstuhl, 2004. Can the activity budget hypothesis explain sexual segregation in desert bighorn sheep? Behaviour **141**:513–520.

Patefield, W., 1981. Algorithm AS159. An efficient method of generating r x c tables with given row and column totals. Journal of the Royal Statistical Society, Series C **30**:91–97.

Pearson, K., 1900. On the criterion that a given system deviations from the probable in the case of correlated system of variables is such that it can be reasonably supposed to have risen from random sampling. Philosophical Magazine **50**:157–175.

R Development Core Team, 2006. R: A language and environment for statistical computing.

Ruckstuhl, K. and H. Kokko, 2002. Modelling sexual segregation in ungulates: effects of groupe size, activity budget and synchrony. Animal Behaviour **64**:909–914.

Ruckstuhl, K. and P. Neuhaus, 2005. Sexual segregation in vertebrates: Ecology of the two sexes. Cambridge University Press.

Ruckstuhl, K. E., 1998. Foraging behaviour and sexual segregation in bighorn sheep. Animal Behaviour **56**:99–106.

Ruckstuhl, K. E. and P. Neuhaus, 2000. Sexual segregation in ungulates: a new approach. Behaviour **137**:361–377.

Ruckstuhl, K. E. and P. Neuhaus, 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. Biological Reviews of the Cambridge Philosophical Society **77**:77–96.

Shank, C. C., 1985. Inter- and intra-sexual segregation of chamois (*Rupicapra rupicapra*) by altitude and habitat during summer. Zeitschrift für Saeugetierkunde **50**:117–125.

Staines, B. W., J. M. Crisp, and T. Parish, 1982. Differences in the quality of food eaten by red deer (*Cervus elaphus*) stags and hinds in winter. Journal of Applied Ecology **19**:65–77.

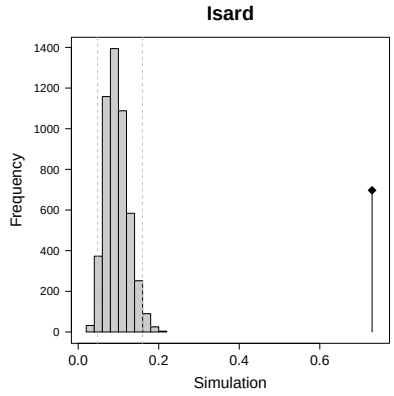
Yearsley, I. and F. Pérez-Barbéria, 2005. Does the activity budget hypothesis explain sexual segregation in ungulates? Animal Behaviour **69**:257–267.

Figure legends

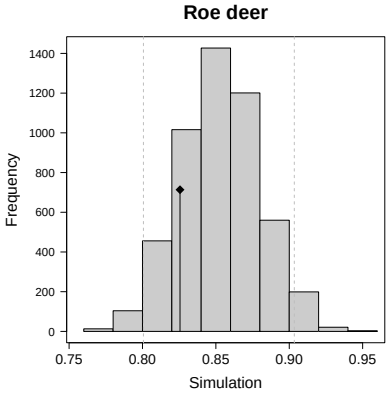
Fig. 1: Permutational distribution of SSAS, observed SSAS (black flag) and 95% confidence limits (grey vertical lines) for a random association of males and females in the case of (a) isard – significant segregation, (b) roe deer – random association and (c) red deer – significant aggregation.

Fig. 2: Annual patterns of sexual segregation / aggregation in isard (a-b), red deer (c-d) and roe deer (e-f) tested using the index of sexual segregation and aggregation (SSAS) (a, c, e), and as given by the segregation coefficient (b, d, f) . The SSAS indicates significant sexual segregation or aggregation if the observed value falls above or below the shaded area (at the 5% error level), respectively. For isard, sexual segregation is high and significant for each month using both the segregation coefficient and the SSAS (a-b). For red deer, significant sexual segregation occurred from April to July in addition to significant sexual aggregation in November, January and February (c) which is similar to the pattern we found with the segregation coefficient (d). By contrast, even though a marked seasonal pattern of group structure in roe deer is shown by SSAS (f), the segregation coefficient suggests no clear pattern over time and apparent sexual aggregation, indicated by negative values. Such a discrepancy arises because the segregation coefficient does not account for solitary animals (Conradt, 1998b).

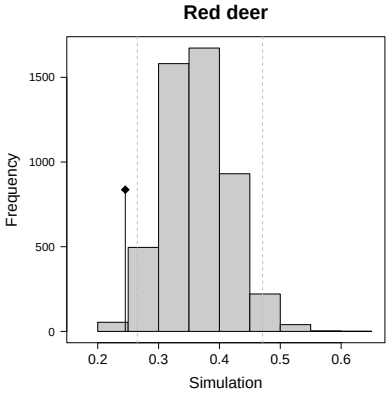
FIG. 1


Isard
Frequency
Simulation
0
200
400
600
800
1000
1200
1400
0.0
0.2
0.4
0.6

(a)

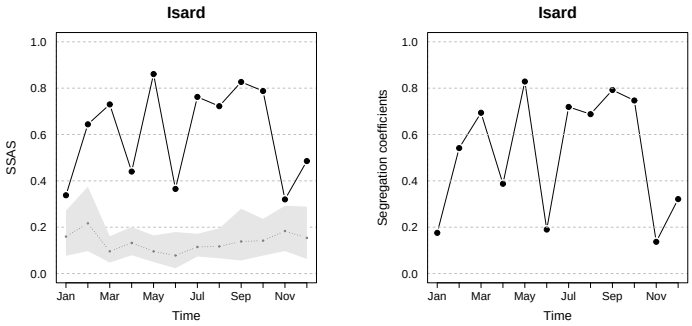

Roe deer
Frequency
Simulation
0
200
400
600
800
1000
1200
1400
0.75
0.80
0.85
0.90
0.95

(b)


Red deer
Frequency
Simulation
0
500
1000
1500
0.2
0.3
0.4
0.5
0.6

(c)

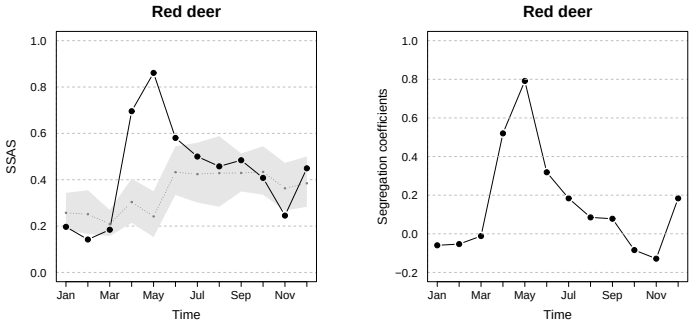
FIG. 2


Isard
SSAS
Time
Jan
Mar
May
Jul
Sep
Nov

(a)

Isard
Segregation coefficients
Time
Jan
Mar
May
Jul
Sep
Nov

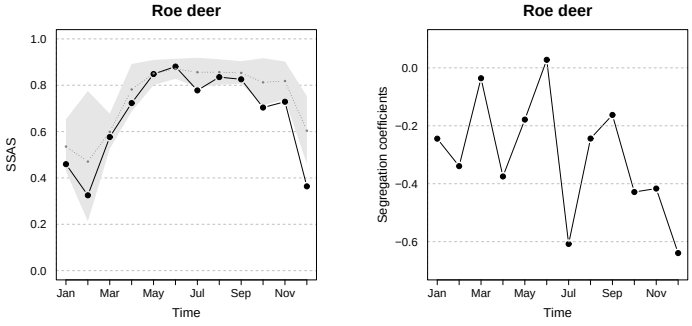
(b)


Red deer
SSAS
Time
Jan
Mar
May
Jul
Sep
Nov

(c)

Red deer
Segregation coefficients
Time
Jan
Mar
May
Jul
Sep
Nov

(d)


Roe deer
SSAS
Time
Jan
Mar
May
Jul
Sep
Nov

(e)

Roe deer
Segregation coefficients
Time
Jan
Mar
May
Jul
Sep
Nov

(f)

Appendix 1: Link between SSAS and SC

The data consist of N individuals (X males and Y females) distributed in k groups. There are N_i individuals in the i-th group: X_i males and Y_i females. Data are organised in a 2 by k contingency table. The traditional χ^2 statistic computed on this contingency table is given by:

$$\boldsymbol{X^2} = \sum_{i=1}^{k} \left(\frac{(X_i - X\,N_i/N)^2}{X\,N_i/N} + \frac{(Y_i - Y\,N_i/N)^2}{Y\,N_i/N} \right)$$

We can then develop this equation as follows:

$$\begin{aligned} \boldsymbol{X^2} &= \sum_{i=1}^{k} \left(\frac{X_i^2 - 2X_i\,X\,N_i/N + X^2\,N_i^2/N^2}{X\,N_i/N} + \frac{Y_i^2 - 2Y_i\,Y\,N_i/N + Y^2\,N_i^2/N^2}{Y\,N_i/N} \right) \\ &= \sum_{i=1}^{k} \left(\frac{X_i^2}{X\,N_i/N} - 2X_i + X\,N_i/N + \frac{Y_i^2}{Y\,N_i/N} - 2Y_i + Y\,N_i/N \right) \end{aligned}$$

Using that $N = X + Y$, $X = \sum_{i=1}^{k} X_i$ and $Y = \sum_{i=1}^{k} Y_i$, we get :

$$\begin{aligned} \boldsymbol{X^2} &= \sum_{i=1}^{k} \left(\frac{X_i^2}{X\,N_i/N} + \frac{Y_i^2}{Y\,N_i/N} \right) - N \\ &= N \left[\sum_{i=1}^{k} \left(\frac{Y\,X_i\,N_i + X\,Y_i\,N_i - N\,Y_i\,X_i}{X\,Y\,N_i} \right) - 1 \right] \\ &= N \left[\sum_{i=1}^{k} \left(\frac{X_i}{X} \right) + \sum_{i=1}^{k} \left(\frac{Y_i}{Y} \right) - \frac{N}{X\,Y} \sum_{i=1}^{k} \left(\frac{X_i\,Y_i}{N_i} \right) - 1 \right] \\ &= N \left[1 - \frac{N}{XY} \sum_{i=1}^{k} \frac{Y_i\,X_i}{N_i} \right] \end{aligned}$$

Consequently, $SSAS = \dfrac{\boldsymbol{X^2}}{N}$. The original formula of the segregation coefficient being $SC = 1 - \dfrac{N}{XY} \sum_{i=1}^{k} \dfrac{X_i\,Y_i}{N_i - 1}$, is intimately linked to the $\boldsymbol{X^2}$/N statistic.