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1 TESTING SEXUAL SEGREGATION AND  
2 AGGREGATION: OLD WAYS ARE BEST

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11 *Abstract.* The study of sexual segregation has received increasing atten-  
12 tion over the last two decades. Several hypotheses have been proposed to  
13 explain the existence of sexual segregation , such as the “predation risk  
14 hypothesis”, the “forage selection hypothesis” and the “activity bud-  
15 get hypothesis”. Testing which hypothesis drives sexual segregation is  
16 hampered, however, by the lack of consensus regarding a formal mea-  
17 surement of sexual segregation. By using a derivation of the well-known  
18 Chi-square (called SSAS) instead of existent segregation coefficients, we  
19 offer a reliable way to test for temporal variation in the occurrence of sex-  
20 ual segregation and aggregation, even in cases where a large proportion

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

13 *Key-words:* Capreolus capreolus; Cervus elaphus; *Chi-square*; Isard; Red  
14 deer; Roe deer; Rupicapra pyrenaica; *Sexual aggregation*; *Segregation co-*  
15 *efficient*; *Sexual segregation*.

## 16 INTRODUCTION

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

1 (Bowyer 2004). However, the degree to which any one of the hypothesis can account  
2 for most observed situations is still unclear (Mooring and Rominger 2004 vs. Neuhaus  
3 and Ruckstuhl 2004; Ruckstuhl and Neuhaus 2002 vs. Yearsley and Pérez-Barbéria  
4 2005).

5 Confusion about sexual segregation terminology (Barboza and Bowyer 2000, Bowyer  
6 2004, Bowyer et al. 1996, Main et al. 1996) and a lack of a general measurement of  
7 sexual segregation hinders our ability to uncover the mechanisms driving the evolu-  
8 tion of sexual segregation. For example, while Conradt (1998) reviewed 3 potential  
9 methods to quantify sexual segregation, additional measurements could have been  
10 used such as Edwards' distance (Edwards 1971), the Overlap index ('D2', Manly  
11 2005) or Nei's distance (Nei 1972). The use of so many indices based on different  
12 metrics has prevented reliable inter-specific or inter-population comparisons despite  
13 the potential pivotal role of such comparisons to our broader understanding of the  
14 evolution of sexual segregation (Myserud 2000).

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

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

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

## 13 DEVELOPING THE SSAS

### 14 *The existing segregation coefficients*

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

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

1 where  $N_i$  is the group size of the  $i$ -th group ( $N_i = X_i + Y_i$ ),  $X$  is the total number  
 2 of males sampled;  $Y$  is the total number of females sampled;  $N$  is the sum of males  
 3 and females sampled. Three limitations arise from the assumptions on which SC  
 4 relies. First, SC is not defined for single animals ( $N_i = 1$ ) because they are thought  
 5 to segregate from their own sex and thus contribute no information about sexual  
 6 segregation (Conradt 1998). However, this restriction may miss some obvious cases  
 7 of sexual segregation. For instance, in the following 5 groups composed of 1, 1, 1, 1,  
 8 1 males and 0, 0, 0, 0, 25 females sexual segregation obviously occurs while the SC  
 9 cannot be calculated. Second, SC can be used only to investigate sexual segregation  
 10 against random association and aggregation per se is not dealt with. Therefore, SC  
 11 values tend to be  $< 0$ , which prevent using a modified formula suggested as more  
 12 appropriate (Conradt 1999). Finally, SC has no test against random association.

### *Linking the segregation coefficient with the SSAS*

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

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

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

1 test for the segregation and aggregation patterns observed in natural population,  
2 even when dealing with solitary animals. The SSAS being linked with Cramér's  
3  $V$ , one of the most popular measures of association between 2 qualitative variables,  
4 SASS varies between 0 and 1, regardless of the size of contingency tables (Agresti  
5 1990). As developed below, the major strength of using the SSAS is its ability to test  
6 the null hypothesis of a random association between sexes against two alternatives,  
7 segregation or aggregation. The expectancy of SSAS is  $(k - 1)/(N - 1)$  (Electronic  
8 Appendix 1) and so is inversely related to the mean group size. Being derived from the  
9  $\chi^2$ , SASS provides an estimate of the distance between the observed and the expected  
10 distributions of males and females under the null hypothesis for a given number of  
11 groups ( $k$ ) and animals ( $N$ ). Consequently, *segregation* is defined as a group by sex  
12 composition which is too far from the one obtained under the null hypothesis and  
13 *aggregation* as a group by sex composition which is too close to the one obtained  
14 under the null hypothesis. Biologically speaking, segregation occurs when the sex  
15 ratio of each group is too different from the population sex-ratio (e.g., with many  
16 unisex groups for instance). Conversely, aggregation occurs when each group has a  
17 sex ratio almost equal to the population sex-ratio.

### 18 *Testing the significance of segregation or aggregation*

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

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

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

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

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



## 1 MATERIAL

2 *The biological models*

3 Isard (*Rupicapra pyrenaica* Bonaparte), red deer (*Cervus elaphus* L.), and roe deer  
4 (*Capreolus capreolus* L.) have contrasting biology and behaviour (Andersen and Lin-  
5 nell 1998, Clutton-Brock et al. 1982). Red deer is a highly dimorphic species with  
6 marked segregation of the sexes. At our study site, the dressed body mass of male  
7 red deer was 30.4% larger than that of females (respectively 80.4 kg and 59.7 kg,  
8 Bonenfant et al. 2002). A recent comparison of two red deer populations (including  
9 this population) with different timing of breeding suggested that both the predation  
10 risk and the activity budget hypotheses could explain segregation at different times  
11 of the year (Bonenfant et al. 2004). Unlike red deer, roe deer are more solitary, form-  
12 ing small groups only during winter (Bideau et al. 1983). Male roe deer were 7.2%  
13 larger than females in our study (average live body mass of 26.1 kg and 24.3 kg).  
14 Although very few studies have been performed on roe deer sexual segregation (but  
15 see Mysterud 1999), we expected only a limited segregation because of the slight  
16 dimorphism in size (Andersen and Linnell 1998). The isard is a mountain ungulate,  
17 whose sexual size dimorphism is intermediate between red and roe deer (Loison et al.  
18 1999). Despite its rather small sexual size dimorphism (average live body mass of  
19 24.7 kg for females and 25.8 kg for males, i.e. a 6.7% dimorphism), social and habitat  
20 segregation of male and female isard have previously been documented in the Alps  
21 (Shank 1985).

22 *The data*

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

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

## 11 RESULTS

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

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

26 In spite of the gregariousness nature of isard (average group size:  $7.84 \pm 7.32$ ),

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

## 6 DISCUSSION

### 7 *Testing or measuring sexual segregation?*

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

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

4 Several mathematical problems undermine the validity of the segregation coeffi-  
5 cients (SC) and here we list some of the most significant. Although presented as a  
6 measure of sexual segregation (Conradt 1998), the SC is not. The expected value  
7 of SC is not 0 but is  $-1/(N - 1)$  (Electronic Appendix 1, Corollary 7) in Conradt  
8 (1998)'s formulation. Similarly, using the corrected formula (Conradt 1999), the ex-  
9 pected value of the SC still does not equal 0 and is ill-defined under  $H_0$  (the sum  
10 under the square root may take negative values: Electronic Appendix 1, Corollary 7).  
11 Hence for both SC formulations, 0 cannot be taken as a baseline for a random associa-  
12 tion of the sexes. Besides, contrary to SASS which is based on the difference between  
13 the observed and the expected distribution of males and females among groups under  
14  $H_0$ , the SC formulation does not call for the expected values of the contingency table.  
15 Consequently, a test of SC does not warrant a test against a random association of  
16 the sexes in all cases (even with a randomization procedure). Lastly, as shown for the  
17 SSAS values, comparing two values of SCs does not provide any information about a  
18 possible difference of sexual segregation. In addition, excluding solitary animals can  
19 yield erroneous results, such as concluding wrongly to a spurious aggregation pat-  
20 tern, as we observed for roe deer (Figs. 2e-f). Clearly, both SC formulations cannot  
21 reliably handle aggregation patterns or be applied to only slightly gregarious species.

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

1 which we cannot conclude whether sexual segregation occurs or not. For isard (Fig.  
2 2b), approximately the same SC value (0.20) is found in June. Following Conradt  
3 (1998)'s approach, sexual segregation should be similar in both species (same value of  
4 SC: 0.2). However, sexual segregation occurs only in isard, but does not in red deer as  
5 the test of SSAS showed (Figs. 2a–c). Such discrepancies between the interpretation  
6 of SC and SSAS emphasise the importance of testing for group patterns rather than  
7 measuring any value.

### 8 *Biological interpretation of SSAS*

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

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

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

### 5 *Conclusion*

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

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### 3 LITERATURE CITED

- 4 Agresti, A., 1990. Categorical data analyses. Wiley – Interscience Publication, New-  
5 York.
- 6 Andersen, R. and J. D. C. Linnell, 1998. Ecological correlates of mortality of roe deer  
7 fawns in a predator-free environment. *Canadian Journal of Zoology* **76**:1217–1225.
- 8 Barboza, P. S. and T. R. Bowyer, 2000. Sexual segregation in dimorphic deer: a new  
9 gastrocentric hypothesis. *Journal of Mammalogy* **81**:473–489.
- 10 Bideau, E., J. Vincent, and F. Maire, 1983. Evolution saisonnière de la taille de  
11 groupe chez le chevreuil en milieu forestier. *Revue d'Ecologie – La Terre et la Vie*  
12 **37**:161–169.
- 13 Bleich, V. C., T. R. Bowyer, and J. D. Wehausen, 1997. Sexual segregation in  
14 mountain sheep: Resources or predation? *Wildlife Monographs* **134**:3–50.
- 15 Bon, R., 1991. Social and spatial segregation of males and females in polyga-  
16 mous ungulates: proximate factors. In F. Spitz, G. Janeau, G. Gonzales, and  
17 S. Aulagnier, editors, *Ongulés/Ungulates 1991. Proceedings of the International*  
18 *Symposium Ongulés/Ungulates 1991*, pages 195–198, Paris. S. F. E. M. P. – I. R.  
19 G. M.
- 20 Bon, R. and R. Campan, 1996. Unexplained sexual segregation in polygamous un-  
21 gulates: a defense of an ontogenetic approach. *Behavioural Processes* **38**:131–154.
- 22 Bonenfant, C., J.-M. Gaillard, F. Klein, and A. Loison, 2002. Sex- and age-dependent

- 1 effects of population density on life history traits of red deer *Cervus elaphus* in a  
2 temperate forest. *Ecography* **25**:446–458.
- 3 Bonenfant, C., L. E. Loe, A. Mysterud, R. Langvatn, N. C. Stenseth, J. M. Gail-  
4 lard, and F. Klein, 2004. Multiple causes of sexual segregation in European red  
5 deer: enlightenments from varying breeding phenology at high and low latitude.  
6 *Proceedings of the Royal Society of London Series B* **271**:883–892.
- 7 Bowyer, R. T., 2004. Sexual segregation in ruminants: Definitions, hypotheses, and  
8 implications for conservation and management. *Journal of Mammalogy* **85**:1039–  
9 1052.
- 10 Bowyer, T. R., 1984. Sexual segregation in southern mule deer. *Journal of Mammal-*  
11 *ogy* **65**:410–417.
- 12 Bowyer, T. R., J. G. Kie, and V. Van Ballenberghe, 1996. Sexual segregation in  
13 black-tailed deer: effect of scale. *Journal of Wildlife Management* **60**:10–17.
- 14 Bramley, P., 1970. Territoriality and reproductive behaviour of roe deer. *Journal of*  
15 *Reproduction and Fertility* **S11**:43–70.
- 16 Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon, 1982. Red deer : behavior  
17 and ecology of two sexes. University of Chicago Press, Chicago.
- 18 Clutton-Brock, T. H., G. R. Iason, and F. E. Guinness, 1987. Sexual segregation  
19 and density-related changes in habitat use in male and female Red deer (*Cervus*  
20 *elaphus*). *Journal of Zoology* **211**:275–289.
- 21 Conradt, L., 1998. Measuring the degree of sexual segregation in group-living animals.  
22 *Journal of Animal Ecology* **67**:217–226.
- 23 Conradt, L., 1999. Social segregation is not a consequence of habitat segregation in  
24 red deer and feral Soay sheep. *Animal Behaviour* **57**:1151–1157.



- 1 Coulson, G., A. MacFarlane, S. Parsons, and J. Cutter, 2006. Evolution of sexual  
 2 segregation in mammalian herbivores: kangaroos as a marsupial models. *Australian*  
 3 *Journal of Zoology* **54**:217–224.
- 4 Darwin, C., 1859. *On the origin of species by means of natural selection or, the*  
 5 *preservation of favoured races in the struggle for life.* John Murray, London.
- 6 Darwin, C., 1871. *The descent of man and selection in relation to sex.* John Murray,  
 7 London.
- 8 Edwards, A., 1971. Distance between populations on the basis of gene frequencies.  
 9 *Biometrics* **27**:873–881.
- 10 Gaillard, J.-M., D. Delorme, J.-M. Boutin, G. van Laere, B. Boisaubert, and  
 11 R. Pradel, 1993. Roe deer survival patterns: a comparative analysis of contrasting  
 12 population. *Journal of Animal Ecology* **62**:778–791.
- 13 Hewison, A., J. Vincent, and D. Reby, 1998. *The European roe deer: The biol-*  
 14 *ogy of success, chapter Social organisation of European roe deer, pages 189–219.*  
 15 *Scandinavian University Press, Oslo.*
- 16 Lancaster, H. O., 1969. *The Chi-squared distribution.* Wiley Publications in Statis-  
 17 tics, New York.
- 18 Loe, L., R. Irvine, C. Bonenfant, A. Stien, R. Langvatn, S. Albon, A. Mysterud,  
 19 and N. Stenseth, 2006. Testing five hypotheses of sexual segregation in an arctic  
 20 ungulate. *Journal of Animal Ecology* **75**:485–496.
- 21 Loison, A., J. M. Gaillard, C. Pélabon, and N. G. Yoccoz, 1999. What factors shape  
 22 sexual size dimorphism in ungulates? *Evolutionary Ecology Research* **1**:611–633.
- 23 Loison, A., C. Toïgo, J. Appolinaire, and J. Michallet, 2002. Demographic processes

- 1 in colonizing populations of isard (*Rupicapra pyrenaica*) and ibex (*Capra ibex*).  
2 *Journal of Zoology* **256**:199–205.
- 3 MacCullough, D., D. Hirth, and S. Newhouse, 1989. Resource partitioning between  
4 sexes in white-tailed deer. *Journal of Wildlife Management* **53**:277–283.
- 5 Main, M. B., F. W. Weckerly, and V. C. Bleich, 1996. Sexual segregation in ungulates:  
6 new directions for research. *Journal of Mammalogy* **77**:449–461.
- 7 Manly, B., 2005. *Multivariate statistical methods: A primer*. Chapman & Hall, Boca  
8 Raton.
- 9 Miquelle, D. G., J. M. Peek, and V. van Ballenberghe, 1992. Sexual segregation in  
10 Alaskan moose. *Wildlife Monographs* **122**:1–57.
- 11 Mooring, M. and E. Rominger, 2004. Is the activity budget hypothesis the holy grail  
12 of sexual segregation? *Behaviour* **141**:521–530.
- 13 Mysterud, A., 1999. Seasonal migration pattern and home range of roe deer (*capre-*  
14 *olus capreolus*) in an altitudinal gradient in southern norway. *Journal of Zoology*  
15 **247**:479–486.
- 16 Mysterud, A., 2000. Diet overlap among ruminants in Fennoscandia. *Oecologia*  
17 **124**:130–137.
- 18 Nei, M., 1972. Genetic distance between populations. *American Naturalist* **106**:283–.
- 19 Neuhaus, P. and K. Ruckstuhl, 2004. Can the activity budget hypothesis explain  
20 sexual segregation in desert bighorn sheep? *Behaviour* **141**:513–520.
- 21 Patefield, W., 1981. Algorithm AS159. An efficient method of generating  $r \times c$  tables  
22 with given row and column totals. *Journal of the Royal Statistical Society, Series*  
23 *C* **30**:91–97.

- 1 Pearson, K., 1900. On the criterion that a given system deviations from the probable  
2 in the case of correlated system of variables is such that it can be reasonably  
3 supposed to have risen from random sampling. *Philosophical Magazine* **50**:157–  
4 175.
- 5 R Development Core Team, 2006. R: A language and environment for statistical  
6 computing.
- 7 Ruckstuhl, K. and H. Kokko, 2002. Modelling sexual segregation in ungulates: effects  
8 of groupe size, activity budget and synchrony. *Animal Behaviour* **64**:909–914.
- 9 Ruckstuhl, K. and P. Neuhaus, 2005. Sexual segregation in vertebrates: Ecology of  
10 the two sexes. Cambridge University Press.
- 11 Ruckstuhl, K. E., 1998. Foraging behaviour and sexual segregation in bighorn sheep.  
12 *Animal Behaviour* **56**:99–106.
- 13 Ruckstuhl, K. E. and P. Neuhaus, 2000. Sexual segregation in ungulates: a new  
14 approach. *Behaviour* **137**:361–377.
- 15 Ruckstuhl, K. E. and P. Neuhaus, 2002. Sexual segregation in ungulates: a compar-  
16 ative test of three hypotheses. *Biological Reviews of the Cambridge Philosophical*  
17 *Society* **77**:77–96.
- 18 Shank, C. C., 1985. Inter- and intra-sexual segregation of chamois (*Rupicapra rup-*  
19 *icapra*) by altitude and habitat during summer. *Zeitschrift für Saeugetierkunde*  
20 **50**:117–125.
- 21 Staines, B. W., J. M. Crisp, and T. Parish, 1982. Differences in the quality of food  
22 eaten by red deer (*Cervus elaphus*) stags and hinds in winter. *Journal of Applied*  
23 *Ecology* **19**:65–77.

- <sup>1</sup> Yearsley, I. and F. Pérez-Barbéria, 2005. Does the activity budget hypothesis explain
- <sup>2</sup> sexual segregation in ungulates? *Animal Behaviour* **69**:257–267.

## FIGURE LEGENDS

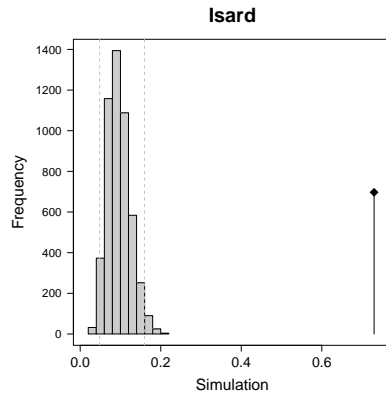
1

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

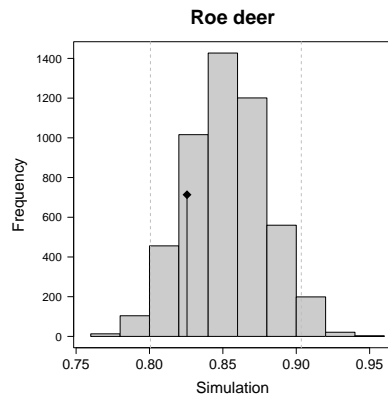
6 FIG. 2: Annual patterns of sexual segregation / aggregation in isard (a-b), red deer  
7 (c-d) and roe deer (e-f) tested using the index of sexual segregation and aggregation  
8 (SSAS) (a, c, e), and as given by the segregation coefficient (b, d, f) . The SSAS indi-  
9 cates significant sexual segregation or aggregation if the observed value falls above or  
10 below the shaded area (at the 5% error level), respectively. For isard, sexual segrega-  
11 tion is high and significant for each month using both the segregation coefficient and  
12 the SSAS (a-b). For red deer, significant sexual segregation occurred from April to  
13 July in addition to significant sexual aggregation in November, January and Febru-  
14 ary (c) which is similar to the pattern we found with the segregation coefficient (d).  
15 By contrast, even though a marked seasonal pattern of group structure in roe deer is  
16 shown by SSAS (f), the segregation coefficient suggests no clear pattern over time and  
17 apparent sexual aggregation, indicated by negative values. Such a discrepancy arises  
18 because the segregation coefficient does not account for solitary animals (Conradt,  
19 1998b).

1

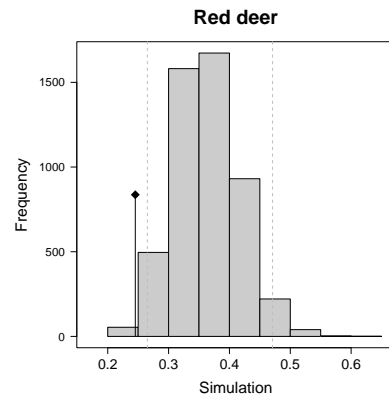
FIG. 1



(a)



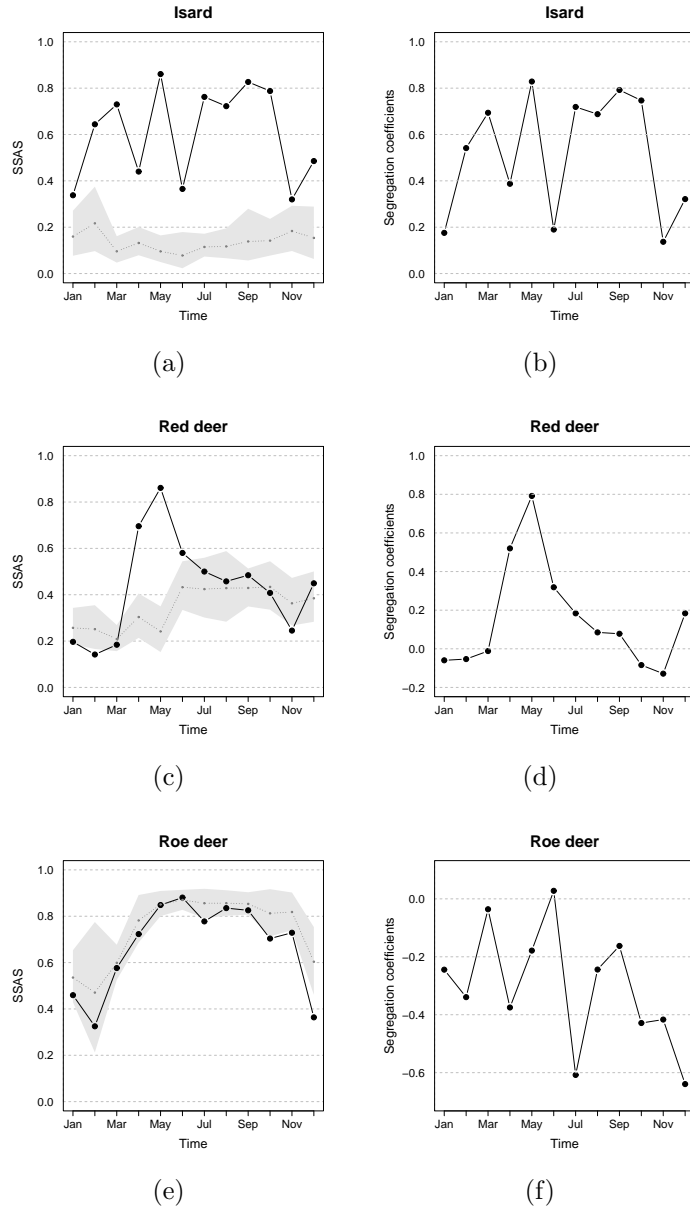
(b)



(c)

1

FIG. 2



## 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  $\chi^2$  statistic computed on this contingency table is given by:

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

We can then develop this equation as follows:

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

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

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

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