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Grouping pattern and specific social preferences in Alpine ibex (*Capra ibex ibex*) with particular attention to the rut

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par

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44 **Résumé**

45

46 La structure sociale d'une espèce donne des informations importantes sur les différents types
47 d'associations entre individus, ainsi que sur le choix du partenaire effectué par les femelles. La
48 structure sociale des ongulés est principalement influencée par la ségrégation sexuelle. Celle-ci est
49 définie par la ségrégation due à l'habitat et aux aspects sociaux. Plusieurs facteurs, comme la
50 différence de la taille entre individus, le système de reproduction, les influences écologiques et aussi
51 la prédation, ont une influence sur la ségrégation sexuelle. En dehors de la période des amours (le
52 rut) les bouquetins des Alpes (*Capra ibex ibex* Linnaeus 1758) s'agrègent en formant des groupes
53 d'individus du même âge et du même sexe. Ces groupes ne se retrouvent pas pendant le rut à cause
54 de la diminution de la ségrégation sociale. Le but de cette recherche est d'étudier la structure sociale
55 des bouquetins des Alpes (population du Parc National Suisse) et les facteurs qui peuvent
56 l'influencer dans différentes périodes de l'année (fin de gestation, naissance, pre-rut et rut). Une
57 attention particulière a été portée sur la période des amours. Pour interpréter l'association entre
58 différentes classes d'individus, la grégarité de chaque classe a été calculée, ce qui a permis
59 d'obtenir la préférence spécifique pour une certaine classe. Des données récoltées entre 1997 et
60 2010 ont été utilisées pour analyser l'association entre différentes classes. L'activité des groupes a
61 été analysée avec les données enregistrées dans le rut du 2009-2010. Avec ces analyses, qui sont les
62 premières effectuées pendant une longue période en ce qui concerne les bouquetins des Alpes, des
63 résultats surprenants ont été trouvés. En observant les différents types de groupes, on remarque que
64 le rut est la période où les groupes mixtes (avec âge et sexe différentes) augment de façon
65 considérable. Par rapport à toutes les autres, les femelles représentent la classe la plus grégaire.
66 Cette classe a une égale préférence sociale pour chaque classe de males pendant le rut. Ces résultats
67 nous montrent que les femelles sont les unités actives dans la formation des groupes et qu'elles
68 effectuent aussi un choix du partenaire.

69 **Abstract**

70 Social structure provides important information about preferred or avoided companionships, thus
71 concerning female partner selection. In polygynous ungulates the social structure is influenced by
72 sexual segregation. Sexual segregation, defined by habitat and social segregation, depends on body
73 size dimorphism, mating system, ecological influences and predation pressures. Alpine ibex (*Capra*
74 *ibex ibex* L. 1758) forms similar age/sex groups outside the mating periods (rut). This pattern is not
75 rescindable during the rut due to the decrease of social segregation. Here I investigated Alpine ibex
76 social structure during different annual periods in the Swiss National Park population, with
77 particular attention to the rut. To interpret the pattern of association, I separated association level
78 into two components: the general gregariousness and the preference for particular classes of
79 associates. I examined patterns of association among age and sex classes using data of 14 years of
80 census (1997-2010) and group time budget using data recorded during the rutting season in 2009-
81 2010. This was the first long-term study about association patterns concerning Alpine ibex and I
82 found surprising results. Females were more gregarious than other classes and had equal social
83 preferences for each class of males during the rut. These results could be evidence that females
84 were the active units in group formation and made mate choice, supported also by the time budget
85 analysis.

86

87 **Key words:** Alpine ibex, *Capra ibex*, social structure, social segregation, specific social preference,
88 groups behaviour, mate choice.

89 **Introduction**

90

91 In gregarious species individuals interact with other individuals at any instant in a group
92 (Whithehead 2008). Animals form a group if they have benefits from aggregation but also when
93 they are attracted by the same stimulus (Ruckstuhl and Neuhaus 2005). Groups change in size and
94 composition during different periods creating different patterns of association level. This affects
95 activity budget of individuals (Conradt 1998; Ruckstuhl and Neuhaus 2001) and the behavioural
96 organization of the society's members, the social structure (Lehner 1996; Pepper et al. 1999). In
97 polygynous ungulates, sexually dimorphic animals, the social structure is principally influenced by
98 the sexual segregation, composed by the habitat- and social- segregation (Bon and Campan 1996;
99 Main et al. 1996; Ruckstuhl and Neuhaus 2005). Animal's age (Bon and Campan 1996), sex, body-
100 size and degree of synchronization (Ruckstuhl and Neuhaus 2001) as well as anti-predator defence
101 strategies (Main et al. 1996), food competition (Alados 1986) and ecological influences
102 (Underwood 1981) may affect sexual segregation. Social segregation depends on differences in
103 behaviour and social motivation. Habitat segregation depends on the use of physical environment
104 (Ruckstuhl and Neuhaus 2005). Ruckstuhl and Kokko (2002) suggested that social segregation
105 leads to habitats segregation, because of this, they have to be treated as independent factors.

106 The social structure of Alpine ibex (*Capra ibex ibex*), a highly dimorphic mountain
107 ungulate, is characterized by the presence of similar age/sex groups outside the mating season
108 (Villaret and Bon 1998) and by parting of these groups during the rut (Niervergelt 1967). Alpine
109 ibex has a strong social segregation (Bon et al. 2001; Villaret and Bon 1995) and great differences
110 in home range for the two genders outside the rut (Grignolio et al. 2004; Parrini et al. 2003). The
111 preferred or avoided companionships in ibex during the rut are still not clear, reflecting the lack of
112 precise understanding of the mating choice of these animals. Mating opportunities in males *Capra*
113 *ibex* are supposed to be strongly age-dependent (Willisch and Neuhaus 2009) and affected also by
114 body mass and horn length (Bergeron et al. 2010).

115 Social segregation describes the division in different social groups due to the facilitation of
116 social learning, inter-class aggression and/or activity synchronisation (Ruckstuhl and Neuhaus
117 2005). It is influenced largely by sexual body size dimorphism, that creates the necessity of each
118 gender to select different grazing sites (Conradt et al. 1999; Jarman 1974; Ruckstuhl and Neuhaus
119 2005). Additionally it is affected by males age (Bon et al. 2001; Festa-Bianchet 1991; Villaret and
120 Bon 1998), climatic weather (Conradt et al. 2000) and decreases drastically during the mating
121 season due to the promiscuous mating system (Bon et al. 2001).

122 The investigation of association patterns (see Ficken et al. 1981; Gowans et al. 2001;
123 Holekamp et al. 1997; Pepper et al. 1999) allows to understand the social structure. Association

124 patterns have still been described with the common association indices (see Cairns and Schwager
125 1987) in ibex outside the mating season (Villaret and Bon 1995) and other polygynous ungulates
126 (bighorn sheep, *Ovis canadensis* L. 1758: Festa-Bianchet 1991; mouflon, *Ovis orientalis musimon*
127 L. 1758: Le Pendu et al. 1995; American bison, *Bison bison* L. 1758: Lott and Minta 1983). These
128 indices do not discriminate the tendency to aggregate with conspecifics in general (general
129 gregariousness) by the tendency to seek certain potential association over other (pairwise affinity)
130 (Pepper et al. 1999). The subdivision of association level separate into these two aspects permits to
131 distinguish the real social preferences of each class (Pepper et al. 1999) and is thus important to
132 understand social structure.

133 The aim of this study was investigated the social structure and the group time budget in the
134 Swiss National Park population of ibex, with particular attention to the rut. This population was
135 reintroduced in 1920 after extinction in the 19th century (Saether et al. 2002). I quantified whether
136 females and classes of males showed a stronger preference to one particular age-sex class during
137 different annual periods. Data from 14 years (1997-2010) of census were used to estimate seasonal
138 patterns of association among natural groups and to study changes in social preferences between
139 and within classes. Data used to investigate time budget were taken during the rutting season in
140 2009-2010. In concordance with previous studies it is expected that ibex females were more
141 attracted by larger males with conspicuous horns during the rut. In addition it is supposed that
142 largest concentration of mixed groups were found during the rut and that each class could change
143 the social preferences during the year, especially in relation to the mating system. In this work I (i)
144 analyse the group size and the structure of the population, (ii) calculate general gregariousness
145 index to measure the tendency to intra- and inter-aggregation, (iii) calculate pairwise affinity index
146 to measure the specific social preferences and (iv) investigate the time budget in groups and
147 individuals during the rut.

148

149 **Methods**

150

151 *Study area*

152 The study was conducted in Val Trupchun (altitudinal range between 1840 and 2220 m above the
153 sea level, 2060 ha), in the south-eastern part of the Swiss National Park (SNP). In SNP the tree line
154 is at 2200 m and the forest is dominated by Swiss stonepine *Pinus cembra* and larch *Larix decidua*.
155 Above the tree line the alpine grasslands and bare rock dominates (Saether et al. 2002). Annual
156 precipitation in Val Trupchun amounts to 700 up 1200 mm. Both sides of the valley are
157 characterised by avalanche runs and couloirs shaped by rock falls, offering additional feeding places

158 for ungulates outside of high-forest areas (Abderhalden and Campell 2006). For further details of
159 the valley refer to Abderhalden and Campell (2006).

160

161 *Animal observation*

162 The studied population consists of 200 to 400 ibex, with variations due to seasonal movements or
163 natural death (e.g. avalanche in winter) (Saether et al. 2002). The census of animal groups was
164 made in different points of the valley during the same day between 1997 and 2010 (Haller 2006).
165 All ibex groups present in the valley during the day of census were registered counting the members
166 and sexing and aging the individual. A group was defined as an assemblage of animals within 50-
167 meters of their nearest neighbour (Toigo et al. 1996) and in visual contact. The sex was determined
168 by horn morphology and the age by the conspicuous annuli of the horns (Ratti and Habermehl
169 1977). Both females and kids were assigned to a class without age or sex discrimination: F and K
170 (Table 1). On the contrary males were assigned to different age classes: M1-3, M4-6, M7-10 and
171 M11+ (Table 1) (Haller 2006). Each year counted at least 4 censuses (January, May, August and
172 November) of the population separated in the group seen (Haller 2006).

173 Behaviour was monitored in 65 groups of Alpine ibex during the rutting periods in 2009-
174 2010. Observations were performed using scan sampling (Altmann 1974). The behaviour of each
175 individual present in group was sampled every 3 min for 1 h 30 min long sessions. Recorded
176 behaviours (according to Schütte-Krug and Filli 2006; Willisich and Neuhaus 2009) were low cost
177 (resting, resting ruminating, standing, grazing), high cost (moving), courtship (low-stretch, tongue-
178 flick, sniff, lick, touch, masturbation, mount, copulation) and agonistic (evasion, flight,
179 displacement, horn contact, horn clash, displacement male). For a brief description of different
180 behaviours see Appendix II. Time budget for each behaviour was determined by the recorded
181 numbers of scans of each behaviour divided by the total recorded number of all the scans.

182

183 *Seasonal designations*

184 Changes in group size and sociality were examined within four annual periods. Annuals periods
185 were determined according to Nievergelt (1974) with some corrections. Late gestation (21st of
186 March to 20th of June); birth -kids born- (21st of June to 30th of August) (according to Ruckstuhl
187 and Neuhaus 2001; Villaret and Bon 1998); pre rut (1st of November to 14th of December)
188 (according to Parrini et al. 2003; Willisich and Neuhaus 2009); and rut (15th of December to 15th of
189 January) (according to Willisich and Neuhaus 2009).

190

191

192 ***Group size and population structure***

193 Ibex social groups were defined according to age categories (Table 2). Group size was calculated by
194 arithmetic mean from field observation and by the ‘Typical Group Size’ (TGS) calculated using all
195 observation of all groups divided into the four annual periods. TGS (Appendix I, expression 1) was
196 an animal-centered measure defined as the sum of the squares of the number in each group, divided
197 by the total number of animals sampled (Jarman 1974). The TGS emphasised the extent to which
198 members of the population tend to associate, which was not revealed by the arithmetic mean.
199 Differences in arithmetic mean and TGS between and within the seasonal designations were tested
200 using χ^2 test.

201

202 ***General gregariousness***

203 To measure the tendency to associate between and within classes, an inter- and intra-class
204 gregariousness index was used (Pepper et al. 1999; Underwood 1981). Inter-class index (C_{ab})
205 indicated the mean proportion of associates with a particular class and it was calculated by
206 summing the number of associates of each class (Appendix I, expression 2). Intra-class
207 gregariousness index (C_{aa}) indicated the mean number of companions of the same class (Appendix
208 I, expression 3). Summing the total of all C_{ab} and C_{aa} values was obtainable the general
209 gregariousness index. This index measured the tendency to aggregate in general of each class and
210 showed if some classes appeared in larger group than other.

211 A permutation test (Manly 1997) was performed to verify if the indices were affected by the
212 annual periods. The inter-class index was asymmetric because members of class a may be
213 accompanied by more members of class b than vice versa. Hence the classes were divided in two
214 groups: seeker and attractor. Seeker corresponded to the classes that searched a possible
215 companions and attractor corresponded to classes that accepted the seeker. Thus each class had two
216 C_{ab} with each other class, because it was calculated both attractor and seeker. C_{ab} as seeker was
217 used to calculate the general gregariousness index of each class, because this was more indicative
218 about the sociality of a class. Besides to analyse the differences of the general gregariousness index
219 of each class between the annual periods a Wilcoxon signed-ranks test was performed.

220

221 ***Specific Social Preferences, Pairwise Affinity Index (PAI)***

222 The specific social preferences among classes were measured using the pairwise affinity index
223 (PAI) (Pepper et al. 1999). This index indicated the level of association for two classes after
224 accounting for the general gregariousness. Important, PAI measured any tendency to associate that
225 was not accounted in general gregariousness. Given that the level of association between classes

226 was affected by their sociability, this index divided the class association index for two classes by
227 the general gregariousness of each to remove its effects (Appendix I, expression 4). Also the intra-
228 class PAI was calculated (Appendix I, expression 5). One-way ANOVA was performed to test if the
229 annual periods and classes influenced the specific social preferences. To test the change of PAI in
230 different annual periods, Fisher's F test was fitted.

231

232 *Time budget*

233 A binomial test was conducted to examine differences in ages of males that made courtship
234 behaviour in different groups. To examine differences in time budget of groups and of each male as
235 a function of sex ratio (total males present in group/total females present in group), proportion of
236 old males (total old males present in group /total males present in group, old males were individuals
237 ≥ 9 years old in accordance with Willis and Neuhaus (2009)), group size and age (variable used
238 only for time budget of males), were employed mixed-effects models using restricted maximum-
239 likelihood method with the three variables (for time budget of males the four variables) as fixed
240 factors and group size as random factors (Haccou and Meelis 1994). All percentages were arcsine
241 square-root transformed to approximate a normal distribution (Zar 1999). Residuals for the
242 restricted maximum-likelihood models were normally distributed.

243

244 All statistical analyses were performed using the R.2.10 statistical package (R Development Core
245 Team 2010).

246

247 **Results**

248

249 Groups size and composition were based on 1861 groups of ibex observed during 14 years
250 and consisting in 49% F, 7% M1-3, 11% M4-6, 17% M7-10, 7% M11+ and 9% K (Table 1). For
251 abbreviation of social group type see Table 2. FK groups were the majority of ibex groups seen
252 (34.6% of all groups sighted). Few M<7 groups were observed (4.9% of all groups sighted)
253 principally because these individuals were inserted in the FM<7 groups (14.5% of all groups
254 sighted). A high number of M \geq 7 groups (17.2% of all groups sighted) and a low number of M
255 groups (9.5% of all groups sighted) were observed. The percentage of different groups varied
256 during the different annual periods (Table 3). Major differences were observed throughout the rut,
257 when a remarkable increase of the number of MX, FM<7 and FM \geq 7 groups (26.2%, 18% and 19%
258 of all groups respectively) and a strongly decrease of FK groups (18.9% compared to 50.8%
259 registered in birth) were recorded.

260 **Group size and population structure**

261 The size of different group types varied between an average of 1.4 to 11.5 individuals. MX group
262 had the higher mean (11.5 individuals in late gestation) and $M \geq 7$ groups the lower (1.4 individuals
263 in rut). Arithmetic mean size of all groups observed changed little during the 4 annual periods
264 (range FK groups = 3.8 to 3.1; $M < 7$ = 2.1 to 1.4; $M \geq 7$ = 2.7 to 1.4; M = 6.8 to 3.2; $FM < 7$ = 8.2 to
265 5.2; $FM \geq 7$ = 6.8 to 5.3; MX = 9 to 11.5) (Fig. 2). Here arithmetic mean size was not corrected by
266 the number of groups seen. The greatest variation in group size occurred among MX groups ($\chi^2 =$
267 8.82; $p = 0.032$; $df = 3$), in which group size was quite high during the rut (mean 10.48) and
268 decreased dramatically during birth (mean 0). Biggest groups (32 to 42 individuals) corresponded to
269 MX groups sighted during the rut. Smallest groups (1 to 2 individuals) were often FK groups
270 sighted during late gestation and also $M \geq 7$ (1 individual) sighted during all the year.

271 No differences were detected in TGS between 4 annual periods ($\chi^2 = 21.18$; $df = 18$; $p =$
272 0.25; TGS max = 16.1 in rut and TGS min = 1.7 in birth) (Fig. 1) and in all the groups types
273 excluded MX. TGS of MX groups varied significantly within the four periods ($\chi^2 = 14.83$; $p =$
274 0.001; $df = 3$). Major changes in group composition occurred during rut and were characterized by
275 an increase of TGS in MX groups and a decrease in other groups.

276

277 **General gregariousness**

278 The coefficient of general gregariousness was significantly affected by the annual periods
279 (permutation test, $F_{obs} = 5.32$, $p = 0.036$), by the seeker (permutation test, $F_{obs} = 11.67$, $p = 0.001$)
280 and by the attractor (permutation test, $F_{obs} = 27.29$, $p = 0.001$). The interaction between this two
281 actors was significant (permutation test, $F_{obs} = 5.82$, $p = 0.001$), principally due to high presence of
282 kids with females (Fig. 3). During the year each class displayed a tendency to remain with
283 companions of the same age and sex. The only exception to this pattern occurred during the rut,
284 when females were found in groups with companions of opposite sex, forming MX groups. In
285 particular the average female in this period had 4.7 M4-6, 4.3 M7-10 and 3.9 M11+ companions,
286 while during the non-mating periods the average female had 1.56 M4-6, 0.63 M7-10 and 0.5 M11+
287 companions. Female class was the only one that changed significantly the general gregariousness
288 between the different annual periods (Wilcoxon signed rank test, rut-birth: $p = 0.031$; rut-pre rut: p
289 = 0.031) and was the most gregarious class (Wilcoxon signed rank test, $p < 0.02$ in all cases).
290 Interestingly, females in rut showed similar preferences for each class of males (23% companions
291 M1-3; 19% M4-6; 18% M7-10; 16% M11+; test of two percentages did not detect significantly
292 differences) (Fig. 3 (a)). Surprisingly, males classes did not show any significant change in general
293 gregariousness between different periods.

294 ***Specific Social Preferences, Pairwise Affinity index (PAI)***

295 The specific preferences for association with particular classes and partners of each classes changed
296 during different annual periods (ANOVA, $F_{obs} = 5.91$, $p = 0.001$; $F_{obs} = 2.23$, $p < 0.001$
297 respectively). Rut was the period during which each class associated with others more than other
298 periods (Fisher's F, $p < 0.001$ in all cases) (Fig. 4). Females displayed strikingly equal preferences
299 to classes of males when in rut, showing an affinity with males equal at the affinity with other
300 females, pattern not detectable in other annual periods. The strongest affinities among classes
301 involved M11+ and M7-10 in non-mating period.

302

303 ***Time budget***

304 Courtship behaviour was present in 49 groups. The 67.39% of males that made courtship behaviour
305 were the oldest males in group (binomial test, $p = 0.02$). The mixed-effects model showed that low
306 cost, courtship and agonistic behaviours were affected by sex-ratio. Interestingly, high cost
307 behaviour increased according to group size (Table 4). Analyses concerning every single male
308 present in a group showed that the courtship and low cost behaviour increase (effect size = 0.03, SE
309 = 0.01, d.f. = 251, t -value = 5.9, $p < 0.001$) and decrease (effect size = -0.02, SE = 0.01, d.f. = 251,
310 t -value = -4.8, $p < 0.001$) with the age, respectively. In contrast, the increasing of old males
311 decreased the agonistic behaviour (effect size = -0.1, SE = 0.04, d.f. = 251, t -value = -2.7, $p =$
312 0.019), but increased the high cost behaviour (effect size = 0.12, SE = 0.06, d.f. = 251, t -value =
313 1.9, $p = 0.019$). Interestingly, agonistic behaviour of males increased according to group size (effect
314 size = 0.01, SE = 0.003, d.f. = 11, t -value = 2.5, $p = 0.035$), same patterns observed in group.
315 Besides in females agonistic behaviour increased with the increasing of sex ratio in groups (effect
316 size = 0.119, SE = 0.031, d.f. = 215, t -value = 3.8, $p < 0.001$).

317

318 **Discussion**

319

320 The most important results of this study about social structure and time budget in ibex were:
321 (1) a largest concentration of mixed groups during the mating season, (2) the prevalence of small
322 groups composed by females and kids outside the rut, instead of old males as suggested by Bon et
323 al. (2001), (3) females were the most gregarious class and the only one changing general
324 gregariousness between different annual periods, (4) females in rut had equal social preferences for
325 each class of males, (5) general gregariousness and social affinity varied during the different annual
326 periods, and (6) high cost behaviour in group increased according to group size.

327 In many dimorphic ungulates, social segregation among sexes is high outside the breeding
328 season, as reported for *Capra ibex ibex* (Nievergelt 1974) and other species (chamois, *Rupicapra*
329 *rupicapra* L. 1758: Perez-Barbeira and Nores 1994; bighorn sheep, *Ovis canadensis*: Geist and
330 Petocz 1977; reindeer, *Rangifer tarandus* L. 1758: Cameron and Whitten 1979; red deer, *Cervus*
331 *elaphus* L. 1758: Conradt 1999; common eland, *Taurotragus oryx oryx* Pallas 1766: Underwood
332 1981). This study provided another detailed example of this trend.

333 However, the present study was the first to provide a detailed investigation in social
334 preferences and in time budget of ibex groups and individuals during the rut. It is also the first study
335 dressed on polygynous ungulates that separate the association index into general gregariousness and
336 pairwise affinity index (Pepper et al. 1999). Previous studies (i.e. Le Pendu et al. 1995; Lott and
337 Minta 1983; Villaret and Bon 1998) investigated the social preferences in ungulates using the
338 commonly association indices as explained by Cairns and Schwager (1987). These indices used to
339 quantify association levels the combined effects of general gregariousness and pairwise affinity
340 index, preventing to distinguish between them (Pepper et al. 1999). Thus they cannot discern the
341 real social preferences. This is because even in the absence of any social preference, members of a
342 more gregarious class will associate with each other more than with members of a more solitary
343 class.

344 During the annual periods the proportion of different social groups changed (Table 3), with
345 major changes occurring between the rut and the other periods. In particular the non reproductive
346 season was characterized by formation of a high number of small FK, $M < 7$ and $M \geq 7$ groups. From
347 previous knowledge on ungulate anti-predator strategies this could be a consequences of the lower
348 predation risk present in SNP (in region with predation risk group size is high, see mountain goats,
349 *Oreamnos americanus* de Blainville 1816: Risenhoover and Bailey 1985; spanish ibex, *Capra*
350 *pyrenaica* L. 1758: Alados 1986). Outside the rut I observed also a high number of $FM < 7$ and $M \geq 7$
351 groups, while few groups were composed by males of different ages. This reflects the necessity of
352 individuals of a compatibilities of activity budget (activity budget hypothesis detailed by Ruckstuhl
353 and Neuhaus (2005)) and a synchronisation due to the similar body size (Conradt 1998; Ruckstuhl
354 1998; Ruckstuhl 1999). On the contrary, the rut was characterized by a strong increase of MX
355 groups, with a consequent change in the sex ratio and decrease of synchronisation due to the
356 presence of different sexes and aged individuals in groups (Ruckstuhl and Neuhaus 2001). This
357 increase of sex ratio affected the activity in groups, decreasing the low cost behaviour and
358 increasing the courtship and agonistic behaviour. The increase presence of mixed groups recorded
359 during the rut was accompanied also by an increase of TGS. This was due to the social factors (see
360 explanation in the next paragraph) that acquired a great importance in groups formation (Alados

361 1986). Stability of arithmetic mean and TGS during the year (found also in Asiatic ibex, *Capra ibex*
362 *sibirica* L. 1758: Fox et al. 1992) were influenced by the life history constraints (e.g. social
363 ontogeny), and by the lack of any type of selective pressure (Lott and Minta 1983). Only one
364 selective pressure presents in Alpine ibex is the formation of strict dominance hierarchies in males
365 before the rut (Willisch and Neuhaus 2010).

366 General gregariousness analyses revealed that females were significantly more gregarious
367 than other classes and became very sociable during the rut. Surprisingly, females did not show any
368 preferences for a specific males class (Fig. 3 (a)). I suggested that they weren't interested by
369 specific age of males. Outside the rut females aggregated with other females rather than with other
370 classes and showed a high association level, due at they higher general gregariousness rather than
371 specific preferences. In contrast, during the rut the association was due principally at the specific
372 preferences. This could indicate that females were the active units in group formation and make
373 mate choice. Females were submitted at the courtship behaviour of older males present in the group,
374 but not necessarily these males were the choice of females. In polygynous ungulates only few
375 studies showed that females actively select or compete for the mating partners (topi antelopes,
376 *Damaliscus lunatus* Burchell 1824: Bro-Jorgensen 2002; red deer, *Cervus elaphus*: Bebie and
377 McElligott 2006). My results revealed that old males ibex increased the high cost behaviour during
378 the rut, because wanted stay at centre of the groups, behaviour indicating a partner selection by
379 females (Bro-Jorgensen 2002). Besides males increased agonistic behaviour (only displacements) in
380 larger groups, maybe to defend their place in group. Increasing of agonistic behaviour in females,
381 due to the increase of sex ratio in group, could show a reject of males that not interest at the females
382 (F.T. personal observation). Willisch and Neuhaus (2010) provide support for a stable dominance
383 relationship between males, therefore it is possible that females have an unavoidable choice in
384 males.

385 Pairwise affinity index (PAI) showed that males developed specific preferences outside the
386 rut, in particular with individuals of the same age or, for yearling males, with females. M11+ had
387 stronger affinity with the same older males. Lower sociality of this class, retained by Bon et al.
388 (2001), was due exclusively to low gregarious. The groups of M11+ were unusual to observe,
389 because they had difficulties to found same aged individuals (Bon et al. 2001). This could indicate
390 that social segregation not increase with the age (as explained by Bon et al. 2001) but was an effect
391 of the population density. Decrease of variation in PAI during the rut was due also to decrease of
392 the habitat segregation during the mating system (Bon et al. 2001; Parrini et al. 2003). Ibex used
393 larger home range in summer and autumn and smaller in winter, because of snow cover (Parrini et
394 al. 2003). Moreover the big differences in movements between sexes increased habitat and social

395 segregation outside the rut (Ruckstuhl and Neuhaus 2001), consequently the high variation in PAI.
396 Several authors suggested that affinities among males were based exclusively on sharing home
397 range (Hall, 1986; Moss and Poole, 1983), but my analysis showed that males, as well as females,
398 had companionship preferences. This explains that more than habitat segregation the sexual
399 segregation is due principally to social segregation.

400 Overall, my study revealed a previously undocumented aspect of Alpine ibex association
401 that concerns the preferential association between females and all males classes during the rut. The
402 largest concentration of mixed groups were, as expected, found during the rut and only females
403 changed social preferences during the year. In conclusions, these results could be evidence of
404 females being the active units in group formation as they act as attractors and selectors of males.

405 Future work should analyze the social interactions during the rut between known individuals
406 that will increase the knowledge about social structure of Alpine ibex and analyze females
407 aggression rates to better understand mating choice.

408

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414 collection.

415 **APPENDIX I**

416 **Typical group size (TGS)**

417 It is defined as:

$$418 \quad T = \frac{\sum_{j=1}^n x_j^2}{\sum_{j=1}^n x_j} \quad (1)$$

422 where T is the typical group size, n are the groups observed of specific social type and x_j is the
423 number of individuals seen in group j .

425 **General gregariousness (GG)**

426 *Inter-class index GG*

$$427 \quad C_{ab} = \frac{\sum_{j=1}^n C_a(j) C_b(j)}{\sum_{j=1}^n C_a(j)} \quad (2)$$

430 where $C_a(j)$ is the number of members of class a in observed group j . b is members of another
431 classes associated with class a .

432 *Intra-class index GG*

$$433 \quad C_{aa} = \frac{\sum_{j=1}^n C_a(j)^2}{\sum_{j=1}^n C_a(j)} - 1 \quad (3)$$

437 **Pairwise Affinity Index (PAI)**

438 *Inter-class index (PAI)*

$$439 \quad PAI_{ab} = \frac{\sum_{j=1}^n C_a(j) C_b(j) * \sum_{j=1}^n s_j (s_j - 1)}{\sum_{j=1}^n C_a(j) (s_j - 1) * \sum_{j=1}^n C_b(j) (s_j - 1)} \quad (4)$$

444 s_j represents the size of group j and $(s_j - 1)$ the total number of associates for each member of group
445 j . The sum of $s_j (s_j - 1)$ indicates the total number of associates summed across all individual
446 present in the periods analyzed.

448 *Intra-class index (PAI)*

$$449 \quad PAI_{aa} = \frac{\sum_{j=1}^n C_a(j) (C_a(j) - 1) * \sum_{j=1}^n s_j (s_j - 1)}{\sum_{j=1}^n C_a(j) (s_j - 1) * \sum_{j=1}^n C_a(j) (s_j - 1)} \quad (5)$$

454 Here the $C_b(j)$ present in inter-class index is replaced with $(C_a - 1)$ because each member of class a
455 has $C_a(j) - 1$ associates members of class a .

456
457

APPENDIX II

458 **Low cost behaviour** (Schütte-Krug and Filli 2006)

459 – *Grazing*: the animal is standing on its four legs, its head remaining below the shoulder, or it
460 moves with lowered head, ingesting forage;

461 – *Standing*: the animal stands still in one place, with its head above the shoulder;

462 – *Resting ruminating*: animal resting on the ground, making clearly visible mandibular movements

463 – *Resting*: animal resting on the ground.

464 **High cost behaviour** (Schütte-Krug and Filli 2006)

465 – *Moving*: any kind of movements in which the animal's head is held above the shoulder.

466 **Courtship behaviour** (Willisch and Neuhaus 2009)

467 – *Low-stretch*: neck straightened and head in plane with the muzzle pointed towards a female;

468 – *Tongue-flick*: flicking with tongue towards a female;

469 – *Sniff*: sniffing a female;

470 – *Lick*: licking a female;

471 – *Touch*: touching a female with the snout;

472 – *Masturbation*: touching penis with snout while standing next to a female;

473 – *Mount*: placing the sternum on the female's back;

474 – *Copulation*: subset of mounts in which the abdomen of the male is firmly pressed against the
475 vulva of the female, resulting in a intromission of the penis.

476 **Agonistic behaviour** (Willisch and Neuhaus 2009)

477 – *Evasion*: walking away from an approaching male;

478 – *Flight*: running away in response to an approaching male;

479 – *Displacement*: driving another male away by slowly approaching it;

480 – *Horn contact*: locking horns with those of another male;

481 – *Horn clash*: hitting the horns against those of another male;

482 – *Displacement male*: female turn out a male that made courtship behaviour.

483
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613 Tables

614

615 Table 1.

616	Class	Abbreviation
617		
618	Female	F
619	Male 1-3 years of age	M1-3
620	Male 4-6 years of age	M4-6
621	Male 7-10 years of age	M7-10
622	Male 11 and more years	M11+
623	of age	
624	Kid	K

625 **Tab 1.** Abbreviation of different classes of ibex. Separation
626 made in function of sex and age.

627

628

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630

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632

633 Table 2

634	Social group type	Abbreviation	Group composition criteria
635	Female/kid	FK	females, kids
636	Male < 7	M<7	males < 7 years
637	Male ≥ 7	M≥7	males ≥ 7 years
638	Male	M	all males
639	Female / Male < 7	FM<7	males < 7 years, females
640	Female / Male ≥ 7	FM≥7	males ≥ 7 years, females
641	Mixed	MX	none of the above
642			
643			
644			

645 **Tab 2.** Criteria used to assign individuals at different social group type.

646

647

648 Table 3

Social group type	Pre rut (n = 563) %	Rut (n = 507) %	Late gestation (n = 521) %	Birth (n = 193) %
FK	36	19	43	51
Male < 7	6	3	5	6
Male ≥ 7	19	15	18	18
Male	14	3	9	13
Female / Male < 7	12	16	18	10
Female / Male ≥ 7	4	18	4	2
Mixed	9	26	3	0

663 **Tab 3.** Percentage of different social group type in
664 annual periods.
665666
667
668
669 Table 4.
670

	Factor	Effect size	SE	d.f.	t-value	P-value
Low-cost behaviour	Sex ratio	-0.162	0.073	45	-2.23	*
	Proportion old males	-0.064	0.085	45	-0.76	†
	Group size	-0.007	0.006	12	-1.23	NS
High-cost behaviour	Sex ratio	0.118	0.059	45	1.99	†
	Proportion old males	0.087	0.071	45	1.22	NS
	Group size	0.011	0.005	12	2.23	*
Courtship behaviour	Sex ratio	0.124	0.074	45	1.68	**
	Proportion old males	0.085	0.087	45	0.98	NS
	Group size	0	0	12	-0.21	NS
Agonistic behaviour	Sex ratio	0.104	0.045	45	2.31	**
	Proportion old males	-0.042	0.053	45	-0.79	NS
	Group size	0.004	0.003	12	1.33	NS

684
685 **Tab 4.** Effects of sex ratio, proportion of old males and group size on
686 time spent in 4 types of behaviour in groups. Restricted maximum-
687 likelihood mixed-effects model: Behaviour, Sex ratio + Proportion old
688 males + Group size+ Group size. Intercepts and random effects
689 Group size are not shown.
690

691 Legend

692

693 **Figure 1.** Arithmetic mean groups size (\pm SE) of data recorded in the field and typical
694 groups size (TGS) of Alpine ibex in the Swiss National Park. Data used were recorded
695 from 1997 to 2010 and separated into four annual periods (pre rut, rut, late gestation
696 and birth). Typical group size (Jarman 1974) is the group size as experienced by a
697 typical individual ibex. Sample size of groups is reported under the legend.

698

699 **Figure 2.** Arithmetic mean groups size (\pm SE) of different social groups types (as
700 reported in Table 3) of Alpine ibex direct observed in the field from 1997 to 2010
701 separated into four annual periods (pre rut, rut, late gestation and birth) in the Swiss
702 National Park. Sample size is reported above the bars.

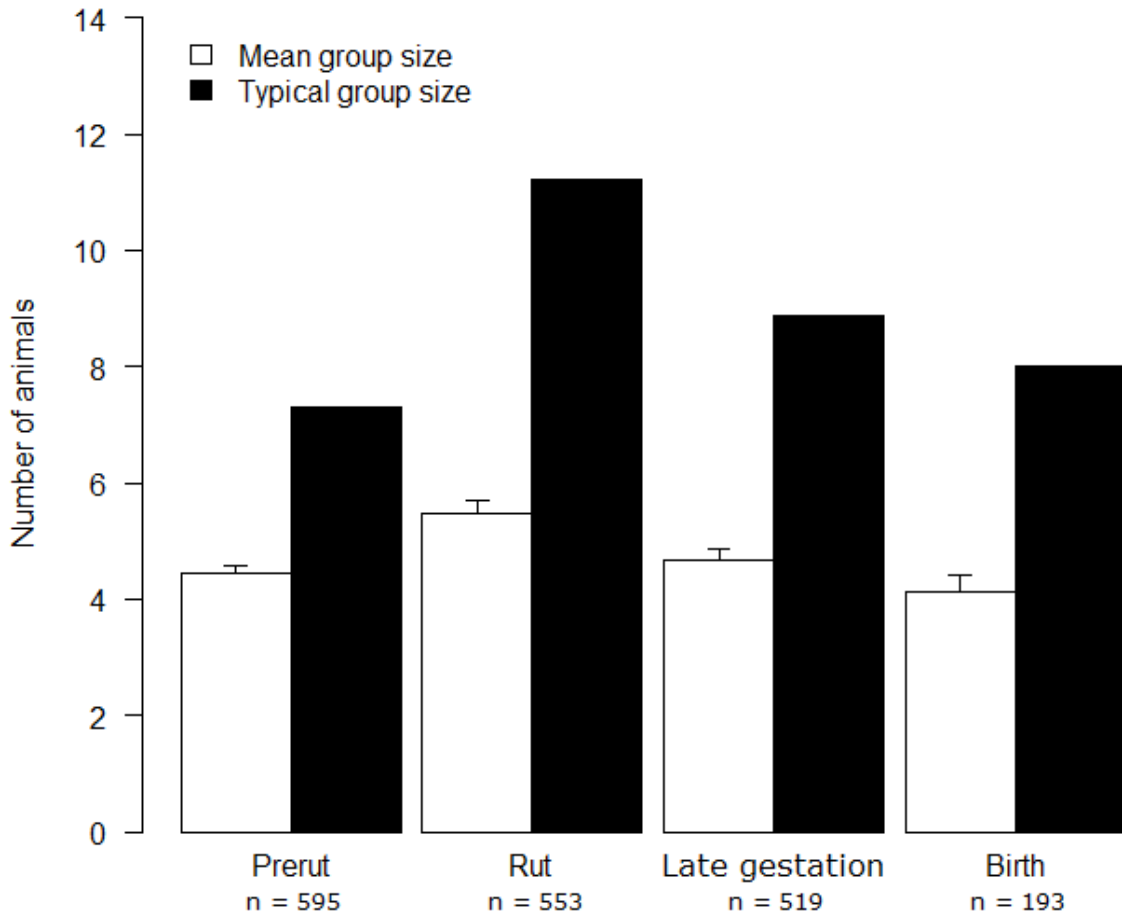
703

704 **Figure 3.** Companions found with specific ibex sex/age classes throughout the year.
705 a) represents the experience of females, b) that of males 1-3 years, c) males 4-6
706 years, d) males 7-10 years, e) males 11+ years, f) kids. Shading shows the
707 proportion of that age/sex classes' companions which were, e.g. females, in a given
708 periods.

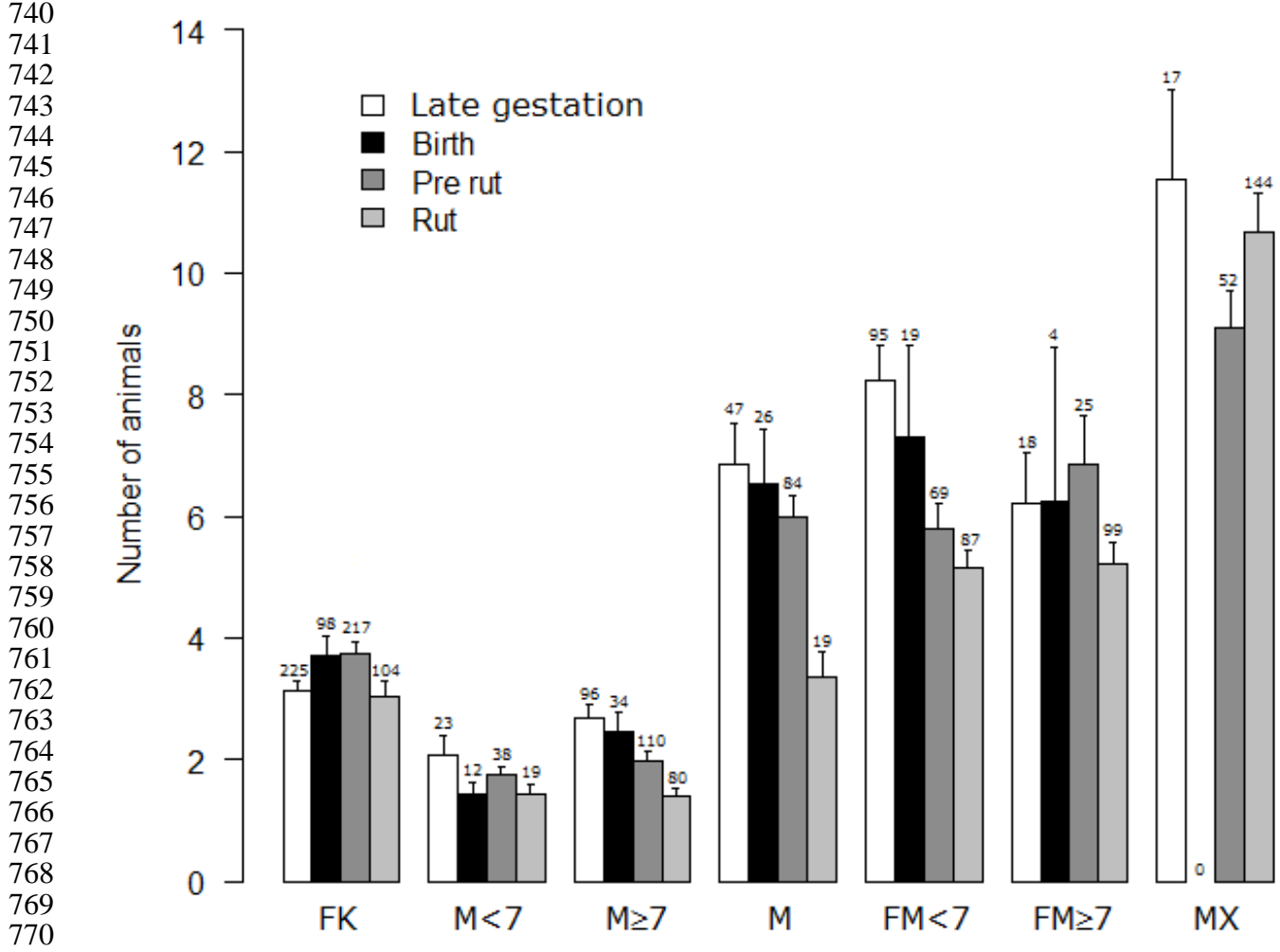
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710 **Figure 4.** Variation in the pairwise affinity index (PAI) observed for each class in pre
711 rut, rut, late gestation and birth. Each column represents the mean PAI of one class.
712 Letter show the equal and different variance.

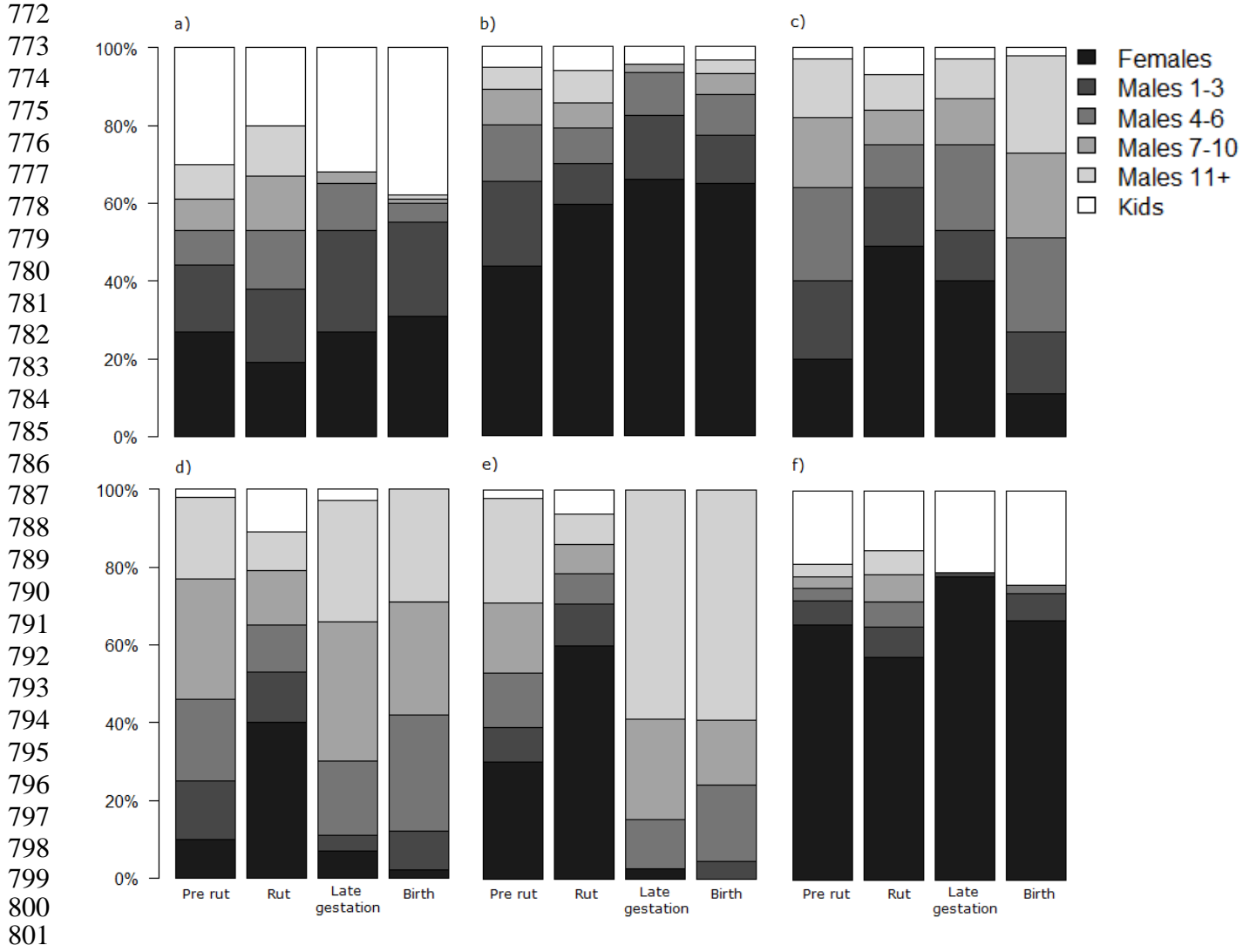
713 Figure 1.



739 Figure 2.



771 Figure 3.



802 Figure 4.

