

1 **The effect of group size, reproductive condition, and time period on sexual segregation**  
2 **patterns in three vespertilionid bat species**

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12 Running header: sexual segregation in roosting bats

13

14 **Abstract**

15 Sexual segregation is widespread across the animal kingdom, yet there is limited consensus on  
16 the factors that shape this behavioural phenomenon. Many of the existing theories are based on  
17 study species with high levels of sexual size dimorphism. Insights from studies on species with  
18 minimal sexual size dimorphism, such as vespertilionid bats, provide an opportunity to study  
19 the factors associated with segregation irrespective of body size effects. Using long-term data  
20 pooled from multiple bat box monitoring schemes across the U.K., we investigated segregation  
21 patterns in maternity roosts of three vespertilionid bat species, Bechstein's bats, *Myotis*  
22 *bechsteinii*, Natterer's bats, *M. nattereri*, and brown long-eared bats, *Plecotus auritus*. We used  
23 the Sexual Segregation and Aggregation Statistic (SSAS) to evaluate temporal trends of sexual  
24 segregation of roosts over the reproductive period (divided into pre-parturition, lactation, and  
25 post-lactation periods). Additionally, we used generalised linear mixed models and beta

26 regression models to investigate the effect of group size on segregation patterns. Our results  
27 showed that the size of the maternity group was an important covariate of inter- and intra-sexual  
28 segregation, with males and non-breeding females typically segregated from large maternity  
29 groups across all three periods. Additionally, we demonstrate that reproductive condition and  
30 period influence segregation patterns, with breeding females segregated from non-breeding  
31 females and males during the lactation period. Although sexual segregation may be caused by  
32 multiple mechanisms, our results show that group size, female reproductive condition, and time  
33 period are key factors associated with segregation within bat roosts. These findings make a  
34 valuable contribution to the understanding of inter- and intra-sexual segregation in  
35 vespertilionid bats and complement existing research on segregation in other mammalian taxa,  
36 providing further evidence that sexual size dimorphism is not a prerequisite for sexual  
37 segregation.

38

### 39 **Keywords**

40 Breeding status, dimorphism, group composition, lactation, sociality, social organization

41

### 42 **Introduction**

43 Sexual segregation, the spatial or temporal separation of males and females (Ruckstuhl, 2007),  
44 is widespread across vertebrate taxa (Ruckstuhl & Neuhaus, 2005; Wearmouth & Sims, 2008).

45 The definition of this behaviour is separated into three potentially overlapping concepts: ‘social  
46 segregation’, whereby the sexes form separate social groups, ‘habitat segregation’, whereby the  
47 sexes differ in their habitat use, and ‘spatial segregation’, whereby the sexes differ in their space  
48 use within homogenous habitat (Ruckstuhl, 2007; Conradt, 1998; Bon & Campan, 1996).

49

50 Multiple hypotheses exist to explain the drivers of this phenomenon, and it is possible that  
51 several factors are involved, and that these can vary across taxa (Ruckstuhl, Clutton-Brock &  
52 Neuhaus, 2005). However, as research into sexual segregation has focussed on sexually  
53 dimorphic taxa, such as ungulates, the effects of body size have become embedded into many  
54 of these hypotheses (Ruckstuhl & Neuhaus, 2000; Bowyer, 2004). For example, as a result of  
55 size dimorphism, males and females may have different nutritional and energetic requirements,  
56 activity budgets, reproductive strategies, or social affinities, which may cause segregation  
57 (Ruckstuhl & Neuhaus, 2002; Ruckstuhl, 1998; Conradt, Ruckstuhl & Neuhaus, 2005; Bon &  
58 Campan, 1996). To understand drivers of sexual segregation independent of the effects of body  
59 size, it is useful to study non-dimorphic species (Ruckstuhl & Neuhaus, 2000). As bats often  
60 segregate, but frequently exhibit less extreme, absent, or reversed (female biased), sexual  
61 dimorphism (Myers, 1978; Williams & Findley, 1979; Stevens, Johnson & McCulloch, 2013),  
62 they are ideal candidate species to investigate factors other than size-dimorphism that might  
63 affect sexual segregation patterns (Ruckstuhl *et al.*, 2005).

64  
65 Bats are characterised by extreme sociability, with diverse social systems encompassing a range  
66 of segregation patterns (Altringham *et al.*, 2005), however research focussing on segregation in  
67 bats is scant compared to other mammalian taxa. Segregation in bats may occur at the roost  
68 level, within the foraging habitat, and at wider spatial scales. Segregation within roosts is  
69 common among many species throughout the nursery season (Altringham *et al.*, 2005),  
70 however there is a lack of evidence to support a generalisable explanation. One leading theory  
71 attributes segregation within roosts to different thermoregulatory and energetic requirements  
72 between the sexes, which are particularly apparent during the reproductive season (May-  
73 September for northern temperate species) (Senior, Butlin & Altringham, 2005; Ruckstuhl *et*  
74 *al.*, 2005; Kerth & van Schaik, 2012). In spring and early summer, reproductive females have

75 higher energetic demands, and require warmer roosts for juvenile development during  
76 pregnancy and lactation, whereas males have lower energy requirements and may further  
77 reduce energy expenditure by entering torpor in cooler roosts (Willis, 2006; Grinevitch,  
78 Holroyd & Barclay, 1995).

79

80 Another proposed explanation relates to competition for foraging areas close to the roost (Kunz,  
81 1974). Lactating females must balance the demands of foraging and returning to the roost to  
82 nurse their young during the night, and are known to forage nearby to the roost (Henry *et al.*,  
83 2002). If males present in the nursery roost share the females' foraging area, as is the case for  
84 some species, e.g. Daubenton's bats (Senior *et al.*, 2005), this increased competition could  
85 compromise the foraging efficiency of females and the survival of their young (Tuttle, 1979;  
86 Altringham *et al.*, 2005). It is unclear if females exclude males from their home range, however  
87 there is evidence demonstrating a higher relative abundance of females compared to males in  
88 higher quality foraging habitat with high prey availability (Lintott *et al.*, 2014; Senior *et al.*,  
89 2005; Russo, 2002; Angell, Butlin & Altringham, 2013; Encarnação *et al.*, 2005). This could  
90 be a result of male exclusion from high quality habitats (Senior *et al.*, 2005; Encarnação *et al.*,  
91 2005), or differential resource use due to the lower energetic needs of males (Levin *et al.*, 2013).

92

93 Whilst both hypotheses are plausible, there are limited empirical data to support them, leaving  
94 scope for alternative interpretations. Furthermore, due to the single species focus of many  
95 existing studies, the factors associated with varying levels of segregation between ecologically  
96 and physically similar species are not apparent. Although the results from these single species  
97 studies have been compared to highlight overall variation (Altringham *et al.*, 2005), there are a  
98 lack of comparative empirical data to explore these differences in detail. Research into inter-

99 and intra-specific variation in segregation may yield important common factors associated with  
100 this behaviour, and inform a more generalisable theory of segregation for bats.

101

102 In this study, we investigated factors associated with inter- and intra-sexual segregation in  
103 maternity roosts of three ecologically similar vespertilionid bat species: Bechstein's bats,  
104 *Myotis bechsteinii*, Natterer's bats, *Myotis nattereri*, and brown long-eared bats, *Plecotus*  
105 *auritus*. These medium-sized vespertilionids display similar low levels of female-biased sexual  
106 dimorphism (<6 % weight difference, this study) and different patterns of sexual segregation,  
107 providing an opportunity to clarify segregation mechanisms independent of the effects of body  
108 size dimorphism. These species are widespread across Europe, with life cycles typical of  
109 temperate zone vespertilionid bats, and colonies displaying fission-fusion sociality  
110 (Fleischmann & Kerth, 2014; Zeus, Reusch & Kerth, 2018). *M. bechsteinii* females roost in  
111 large sexually segregated maternity groups (Kerth & Morf, 2004; Kerth & Petit, 2005; Kerth,  
112 Safi & König, 2002), while in *M. nattereri*, both mixed groups and segregated groups are  
113 common (Altringham, 2014; Funakoshi, 1991; Park, Masters & Altringham, 1998; August *et*  
114 *al.*, 2014). In contrast, *P. auritus* differs from most other temperate zone vespertilionids, as  
115 there is no evidence of sexual segregation in maternity groups during the breeding period  
116 (Entwistle, Racey & Speakman, 1997, 2000).

117

118 Roosting within maternity groups involves a trade-off between costs and benefits: benefits  
119 include social thermoregulation, reduced risk of predation, and social benefits of co-operation  
120 and information transfer (Altringham *et al.*, 2005), whilst costs include parasite and disease  
121 transmission (Lourenço & Palmeirim, 2007; Brown & Brown, 1986), and resource competition  
122 (Krause & Ruxton, 2002). These trade-offs vary with species, sex, breeding status, and between  
123 reproductive periods. For instance, breeding females benefit from social thermoregulation and

124 are known to roost together (Kerth & König, 1999; Kerth & van Schaik, 2012). However, due  
125 to the different physiological requirements of males and non-reproductive females, compared  
126 to reproductive females, and the additional costs of high parasite load in maternity roosts, non-  
127 reproductive bats would be expected to maximize their own fitness by segregating from  
128 maternity roosts and entering torpor (Pretzlaff, Kerth & Dausmann, 2010; Lourenço &  
129 Palmeirim, 2007). Furthermore, as ectoparasite load is known to peak during the lactation  
130 period, and is particularly prevalent among vulnerable juveniles and breeding females with  
131 reduced immune and behavioural defences (Christe, Arlettaz & Vogel, 2000; McLean &  
132 Speakman, 1997; Speakman, 2008), higher levels of segregation may be expected during this  
133 period (Lourenço & Palmeirim, 2007).

134

135 The resulting size of the group is also a consequence of this trade-off between costs and benefits  
136 (Silk, 2007). As group size increases, costs such as higher parasite load, or risk of disease  
137 transmission, increasingly outweigh benefits of group living (Côté & Poulin, 1995; Krause &  
138 Ruxton, 2002). Furthermore, with increased levels of social warming in larger groups, the  
139 temperatures would be too high for non-reproductive bats to enter torpor. Therefore, we expect  
140 increased inter- and intra-sexual segregation in larger groups, as males and non-breeding  
141 females avoid the increased costs. Moreover, breeding females found in smaller roosts may not  
142 reap the full rewards of group living, e.g., social thermoregulation, and consequently may be  
143 driven to roost in larger groups under these conditions (Thirgood, 1996). Therefore, we expect  
144 group size to be an important covariate of inter- and intra-sexual segregation for bats.

145

146 Although assortative mixing among vespertilionid bats has previously been described (Zeus *et*  
147 *al.*, 2018; Patriquin *et al.*, 2010), the factors associated with overall roost segregation are poorly  
148 understood. Comparative empirical data drawn from multiple species are key to an improved

149 understanding of segregation in bats, providing support to a growing body of work studying  
150 this phenomenon (Altringham *et al.*, 2005). Furthermore, whilst group size is known to  
151 influence segregation in other mammalian species (Thirgood, 1996), this factor has not  
152 previously been explored in bats, despite their propensity to form large groups. In this study,  
153 we used a long-term individual-based dataset drawn from multiple bat box monitoring schemes  
154 in southwest England to investigate the influence of group size, reproductive condition, and  
155 time period on inter- and intra-sexual segregation patterns in maternity roosts of three  
156 ecologically and physically similar species. This study aimed to test the following predictions:

- 157 i) breeding females will segregate from non-breeding females and males,
- 158 ii) inter-sexual (between males and females) and intra-sexual (between breeding  
159 and non-breeding females) segregation will be highest during the lactation  
160 period, and
- 161 iii) larger maternity groups will have higher levels of inter- and intra-sexual  
162 segregation.

163

## 164 **Materials and methods**

165 Data used in this study were pooled from separate bat box monitoring schemes across eight  
166 sites in southwest England, collected between 1998 and 2018. The sites were predominantly  
167 heterogenous deciduous woodland with varied species composition and mixed management  
168 histories. Surveys were conducted by licensed bat workers and trainees under their direct  
169 supervision, all under separate English Nature/Natural England project licenses. Each scheme  
170 monitored at least one of our three target species (*M. bechsteinii*, *M. nattereri*, and *P. auritus*)  
171 through surveys of artificial bat roosts (Table 1). Due to the long-term nature of the monitoring  
172 schemes, we were satisfied that bats observed roosting in boxes were representative of the  
173 population at each site. Surveys occurred during the spring, summer, and autumn months. No

174 surveys occurred during the winter months as the bats were not detectable during this time.  
175 Data collection complied with ASM guidelines for research on live animals (Sikes & Gannon,  
176 2011).

177

178 Bats were ringed (banded) on first capture using 2.9 mm aluminium rings (Bat Conservation  
179 Trust, UK, under licence from the SNCO) and age, sex, and reproductive status were  
180 determined in the hand using protocols described in (Linton & Macdonald, 2018). Bats were  
181 categorised as juveniles or adults, and roost groups containing bats that could not be confirmed  
182 as juvenile or adult were removed from our analyses. Females were categorised as breeding  
183 females (BF) if they were recorded as lactating until the post-lactation period that year. Pregnant  
184 bats whose outcome was unknown (only seen during the pre-parturition period that year) were  
185 also classified as BF. Females were categorised as failed or non-breeders (FoNB) if they were  
186 observed during the lactation period in a post-lactating condition, or without enlarged nipples.  
187 Roost groups containing adult females of unknown reproductive status that breeding season  
188 were excluded from the analyses. Only roosts where the full group composition (sex, age class,  
189 and reproductive status of females) of all bats present was known were used in analyses of  
190 segregation and aggregation (Table 2).

191

192 To demonstrate the levels of sexual size dimorphism across the species, we used body weight  
193 measurements, recorded using a spring balance to the nearest 0.1 g. We used measurements of  
194 adult bats with known breeding status and age. Individuals had between 1-29 repeated  
195 measurements (mean  $3.33 \pm 3.24$  SD) over the study period. Our dataset comprised 83 *M.*  
196 *bechsteinii* (72 female, 11 male), 1868 *M. nattereri* (1275 female, 593 male), and 659 *P. auritus*  
197 (307 female, 352 male) body weight measurements.

198

199 *Statistical analyses*

200 Statistical analysis was performed in R (R Core Team, 2019). To assess levels of sexual size  
201 dimorphism in each species, we used a linear mixed effects model using the R package “lme4”  
202 (Bates *et al.*, 2015). Fixed effects included species, sex, reproductive status, and age, with  
203 individual ID and year as random intercept effects to account for repeated measures of  
204 individuals and variation between years. Age was calculated as years since capture for  
205 individuals initially captured as juveniles, with bats of unknown age removed from the analysis.  
206 We compared models to the null hypothesis model using ANOVA, and identified the top model  
207 candidate using Akaike Information Criterion scores (AIC). Visual inspection of diagnostic  
208 plots confirmed homogeneity of variances and normally distributed residuals. Significance of  
209 random effects was tested using likelihood ratio tests.

210

211 We used the Sexual Segregation and Aggregation Statistic (SSAS) (Bonenfant *et al.*, 2007) to  
212 assess sexual segregation and aggregation patterns of roosts. This simple index, derived from  
213 the chi-square statistic, is widely used to study segregation patterns in a variety of vertebrate  
214 species (Wang *et al.*, 2018; Hawkins *et al.*, 2019; Singh *et al.*, 2010; Ficetola, Pennati &  
215 Manenti, 2013). SSAS provides an index value between 0 (complete aggregation) and 1  
216 (complete segregation), according to the following equation:

217

218 
$$SSAS = 1 - \frac{N}{XY} \sum_{i=1}^k \frac{X_i Y_i}{N_i}$$

219

220 Where, for  $k$  groups,  $X$  is the total number of animals sampled in class X, and  $Y$  is the total  
221 number of animals sampled in class Y, and  $N$  is the sum of animals sampled in both classes, X  
222 and Y. This statistic can be used to assess segregation between sexes, or between different

223 classes, based upon breeding status and age, even when a large proportion of animals are  
224 observed alone (Wang *et al.*, 2018; Ficetola *et al.*, 2013; Bonenfant *et al.*, 2007). A  
225 randomization procedure (10,000 permutations) was used to build a distribution of SSAS under  
226 the null hypothesis of random association between classes, which was compared to the observed  
227 statistic using a significance level with a Bonferroni correction ( $\alpha = 0.00833$ ) to account  
228 for multiple comparisons (Bonenfant *et al.*, 2007). To assess segregation by reproductive period  
229 we divided our roost dataset into three reproductive periods: pre-parturition (PP), lactation (L),  
230 and post-lactation (PL), and calculated the statistic separately for each period. These periods  
231 were assigned separately for each roost according to the reproductive status of breeding  
232 females, and presence of juveniles.

233

234 To test for differences in maternity group size between species and reproductive periods, we  
235 used a generalised linear model (GLM) with a Poisson error distribution, as is commonly done  
236 for count data (Warton *et al.*, 2016). Maternity roosts were classified as any roost containing  
237 multiple females with at least one reproductive female. Fixed effects included reproductive  
238 period (PP, L, and PL), and species. We tested the significance of random intercept effects of  
239 box type and year using likelihood ratio tests and found these to be insignificant ( $p = 1$ ), so we  
240 did not include random effects in the model. We compared models to the null hypothesis model  
241 using ANOVA and identified the top model candidate using Akaike Information Criterion  
242 scores (AIC).

243

244 To examine the influence of maternity group size on segregation patterns, we extracted the  
245 maternity roosts that had one or more adult males present ( $n = 216$  groups) and fitted a  
246 generalised linear model with proportion of adult males in the group as the response variable  
247 and maternity group size as a fixed effect. As the response was a proportion, we used a beta

248 regression structure for the model using the R package “betareg” (Ferrari & Cribari-Neto,  
249 2004). As “betareg” does not allow for random effects, we also examined resulting models with  
250 species, period, box type, and year included as fixed effects to ensure these effects do not  
251 strongly influence the resulting coefficients. This process was repeated with proportion of non-  
252 breeding females in the maternity group as the response variable (n = 384 groups).

253

254

## 255 **Results**

### 256 *Sexual size dimorphism*

257 The top model incorporated species, sex, and reproductive status as fixed effects, and individual  
258 ID and year as random intercept effects (Table 3). The likelihood ratio test confirmed the  
259 significance of these random effects ( $p < 0.001$ ). The difference in mean body weights between  
260 non-breeding females and males ranged from 0.14 g (1.7 % difference) in *M. bechsteinii*, 0.41g  
261 (5.2% difference) in *P. auritus*, and 0.44 g (5.7% difference) in *M. nattereri*,

262

### 263 *Temporal patterns of segregation and aggregation in roost composition*

264 Sexual segregation occurred in all three species (Fig 1). Sexual segregation was highest in *M.*  
265 *bechsteinii* roosts, and lowest for *P. auritus* roosts. Breeding females (BF) were segregated  
266 from males across all three reproductive periods in *M. bechsteinii* and *M. nattereri* roosts, but  
267 only during the lactation period in *P. auritus* roosts. Failed or non-breeding females (FoNB)  
268 were segregated from males across all three periods in *M. bechsteinii* roosts, only during the  
269 lactation period in *M. nattereri* roosts, but did not segregate from males across any of the  
270 periods in *P. auritus* roosts. Segregation between BF and FoNB occurred across all periods in  
271 *M. bechsteinii* roosts, but only during the pre-parturition and lactation periods for *M. nattereri*  
272 and *P. auritus* roosts.

273

#### 274 *Maternity roost group size*

275 The top model incorporated species and period as fixed effects, and an interaction effect of  
276 period and species (Table 4). Species was a significant predictor of group size, with *M.*  
277 *bechsteinii* having a positive effect, compared to negative effects of *M. nattereri* and *P. auritus*.  
278 Reproductive period was also a significant predictor, with the pre-parturition and post-lactation  
279 periods having a negative effect on group size. There was a significant interaction effect  
280 between period and species for the pre-parturition period (Table 4), with an interaction plot  
281 showing a steeper increase in group size between the pre-parturition and lactation periods for  
282 *M. bechsteinii*, compared to *M. nattereri* and *P. auritus* (Fig 2).

283

284 The results of the beta regression model for proportion of males showed that maternity group  
285 size was negatively associated with the proportion of adult males found in maternity groups  
286 (coefficient = -0.041, SE = 0.0041,  $p < 0.001$ ) (Fig 3). The pseudo R-squared for this model  
287 was 0.40. Group size had a similar coefficient and p-value when species, period, box type,  
288 and/or year were included as fixed effects in this model (coefficients ranged -0.037 to -0.042,  
289 all with p values below 0.001). The beta regression model for proportion of non-breeding  
290 females in the group also showed that maternity group size was negatively associated with the  
291 proportion of non-breeding females found in maternity groups (coefficient = -0.027, SE =  
292 0.0028,  $p < 0.001$ ), with a pseudo R-squared of 0.20 (Fig 3). Similarly, inclusion of species,  
293 period, box type, and/or year as fixed effects had limited effects on the coefficients (coefficients  
294 ranged -0.027 to -0.031, all with p values below 0.001).

295

296

## 297 **Discussion**

298 Many factors associated with sexual segregation in vertebrates are poorly understood, and are  
299 frequently intertwined with the effects of sexual size dimorphism present in the most common  
300 study systems (Ruckstuhl & Neuhaus, 2000). Therefore, insights from bat species, with limited  
301 size dimorphism, provide a valuable opportunity to clarify segregation mechanisms,  
302 independent of body size dimorphism. Our results showed that the size of the maternity group  
303 was an important covariate of inter- and intra-sexual segregation, with males and non-breeding  
304 females typically segregated from large maternity groups across all three time periods.  
305 However, the lower levels of segregation detected within smaller maternity groups indicate  
306 potential benefits of mixing. Additionally, we demonstrated that time period influenced  
307 segregation patterns, with peaks in segregation during the lactation period.

308

309 Maternity group size was an important covariate of inter- and intra-sexual segregation across  
310 all three periods, and corresponded with overall levels of segregation across the three species,  
311 with *M. bechsteinii* having the largest group size and the most pronounced segregation, and *P.*  
312 *auritus* having the smallest group size and lowest segregation indices. High group size limits  
313 the benefits that non-breeding bats obtain from group living, and increases costs such as  
314 contagious parasites and disease, and competition for food (Krause & Ruxton, 2002; Côté &  
315 Poulin, 1995). Furthermore, with increased social warming in larger groups, non-breeding bats  
316 would not be able to enter torpor to save energy. Group size explained more variation in  
317 segregation for males than for non-breeding females from maternity groups. The low R-squared  
318 value for non-breeding females indicates that other factors are more important in explaining  
319 this variation in segregation, for example, relatedness and social bonds (Zeus *et al.*, 2018).

320

321 The negative relationship between group size and the presence of non-breeding bats could be  
322 an outcome of differing thermoregulatory requirements, as smaller groups with lower levels of

323 social warming may allow non-breeding bats to enter torpor. However, with their differing  
324 thermoregulatory requirements, and the additional costs associated with maternity roosts, males  
325 and non-breeding females would be expected to segregate completely from maternity roosts  
326 under this hypothesis. Furthermore, males do not benefit from torpor throughout the whole  
327 reproductive period. Social thermoregulation facilitates spermatogenesis in males (Entwistle,  
328 Racey & Speakman, 1998), which predominantly occurs during the lactation period for *P.*  
329 *auritus* (Entwistle *et al.*, 1998) and *M. bechsteinii* (Dietz & Hörig, 2011), and during the post-  
330 lactation period for *M. nattereri* (Linton & Macdonald, 2020). With benefits to be gained from  
331 social thermoregulation during this period, males may be expected to avoid costly maternity  
332 groups and form male groups to facilitate spermatogenesis, which is not observed in our study  
333 systems. Therefore, the consistent negative trend of group size and male presence in the  
334 maternity roosts across the whole time period does not lend complete support to this  
335 thermoregulatory argument, suggesting other factors are involved.

336

337 Our observations of non-breeding bats in small maternity groups throughout the reproductive  
338 period suggest that there are additional benefits to roosting alongside females that outweigh the  
339 costs for some individuals. Another potential benefit for males is increased breeding  
340 opportunities with females in the roost (Senior *et al.*, 2005; Angell *et al.*, 2013). Mating may  
341 occur from August to April, with females storing the sperm until fertilization occurs in the  
342 spring (Oxberry, 1979). Evidence shows that male Daubenton's bats roosting alongside females  
343 have increased mating success compared to segregated males (Senior *et al.*, 2005; Angell *et al.*,  
344 2013), suggesting that males mating early in the nursery roost may have improved sperm  
345 storage in the oviduct, leading to greater mating success. These advantages may contribute to a  
346 subtle shift in the cost-benefit tradeoff, leading to reduced segregation during the post-lactation  
347 period. Overall, group size may be one of many factors involved in the cost-benefit tradeoff for

348 mixed group living, with the costs from higher group sizes tipping the balance towards  
349 segregation.

350

351 Breeding females benefit greatly from group living, and when they are present in lower  
352 densities, they may need to roost alongside nonbreeding bats to obtain the full benefits of group  
353 living. Therefore, an alternative, but not mutually exclusive, explanation for decreased  
354 segregation within smaller groups relates to population density. This concept has been  
355 demonstrated in studies on ungulates with low population densities and low proportions of  
356 females that show increased frequencies of mixed sex groups (Meldrum & Ruckstuhl, 2009;  
357 Thirgood, 1996).

358

359 We identified a consistent temporal trend of highest levels of inter- and intra-sexual segregation  
360 during the lactation period. Whilst group size was highest during this period, this peak in sexual  
361 segregation may also be related to the additional costs associated with the lactation period,  
362 including increased competition for food, and high parasite loads due to the vulnerability of  
363 reproducing females and juveniles to parasites (Christe *et al.*, 2000; Lourenço & Palmeirim,  
364 2007). Ectoparasites found on vespertilionid bats include fleas (Ischnopsyllidae), mites  
365 (Spinturnicidae, Macronyssidae, Sarcoptidae, Trombiculidae), batflies (Nycteribiidae), bugs  
366 (Cimicidae), and ticks (Ixodidae, Argasidae) (Zahn & Rupp, 2004). Parasites are particularly  
367 prevalent in maternity roosts due to the reduced immune defence of juveniles and breeding  
368 females (Christe *et al.*, 2000), and the low frequency of grooming behaviour, an activity that  
369 aids removal of ectoparasites, in lactating females (Speakman, 2008) and their offspring  
370 (McLean & Speakman, 1997). Reduced grooming behaviour in juveniles may be related to their  
371 inability to perform this activity (McLean & Speakman, 1997), whilst grooming may be  
372 reduced in lactating females to release energy for lactation (Speakman, 2008). Our analysis of

373 temporal patterns revealed that *P. auritus* exhibit inter- and intra-sexual segregation during the  
374 pre-parturition and lactation periods, a novel insight into the roosting behaviour of this common  
375 and widespread species which is typically described as non-segregating in the literature  
376 (Entwistle *et al.*, 2000).

377

378 Analysis of body weight data confirmed that sexual dimorphism in our study systems was low  
379 (<6 % weight different between non reproductive bats), and showed minimal correspondence  
380 with levels of sexual segregation, with the species showing the least size dimorphism (*M.*  
381 *bechsteinii*) demonstrating the most pronounced sexual segregation. Whereas in ruminants  
382 pronounced sexual size dimorphism can strongly impact factors such as energetic requirements,  
383 metabolic rates, predator vulnerability, and activity budgets (Ruckstuhl & Neuhaus, 2000), we  
384 did not expect the marginal levels of dimorphism present in our study species to strongly impact  
385 these factors.

386

387 Overall, our study identified several factors associated with segregation patterns in bats, lending  
388 support to a variety of hypotheses for the ultimate cause of segregation. For instance, the  
389 patterns of segregation we observed would be expected if segregation mechanisms are related  
390 to different thermoregulatory requirements between different classes (sex and breeding status),  
391 which is among the leading hypotheses (Altringham *et al.*, 2005). However these same patterns  
392 are also congruent with predictions from the activity budget hypothesis, which states that  
393 differences in activity budget synchronization can lead to social segregation (Ruckstuhl, 2007).  
394 With their higher energetic needs, reproductive females would be expected to spend a greater  
395 time foraging compared to the other classes (McLean & Speakman, 1999). Foraging patterns  
396 and roost emergence times may vary according to factors such as sex and reproductive  
397 condition (Kunz, 1974), therefore, segregated day roosts could be a result of reproductive

398 females synchronizing their activity budgets, exiting and returning to roosts at similar times. It  
399 is possible that many different factors interact, including thermoregulatory requirements,  
400 parasite load, resource competition, and access to mating opportunities, that together determine  
401 the levels of segregation within roosts.

402

403 An explanation for interspecific differences in sexual segregation patterns is still required for  
404 these three species. With their similar physiological characteristics, differences in  
405 thermoregulatory and energetic requirements cannot explain the different patterns observed  
406 between these species. One potential explanation relates to competition for foraging areas close  
407 to the roost (Kunz, 1974). Reproductive females have high energy demands, and require high  
408 quality foraging habitat in close vicinity to the roost (Henry *et al.*, 2002). *P. auritus* males are  
409 known to forage on the edge of the foraging habitat of the females (Entwistle *et al.*, 1997), and  
410 therefore pose less competition compared to males that share the same foraging grounds (such  
411 as Daubenton's bats). This sex-based difference in foraging activity could explain the decreased  
412 levels of segregation observed for this species (Altringham *et al.*, 2005). Overlap in foraging  
413 area between the sexes reaches 46% in *M. bechsteinii* (Kerth & Morf, 2004), and is less well  
414 studied for *M. nattereri*. Comparative data on sex-based foraging activity may shed light on the  
415 differences in roost segregation patterns observed between vespertilionid bat species.

416

417 Due to the marginal levels of sexual size dimorphism in our study species, we were able to  
418 highlight important factors in sexual segregation mechanisms, independent of the effects of  
419 body size, namely group size, female reproductive condition, and time period. Whilst  
420 reproductive condition and period have been included in previous studies on roost segregation  
421 (Patriquin *et al.*, 2010; Zeus *et al.*, 2018), maternity group size has not been considered  
422 previously. This factor was a significant covariate of segregation across all three species, and

423 additionally corresponded with the interspecific differences in segregation that were also  
424 observed. Due to the cost-benefit tradeoff associated with roost size, it is likely that this factor  
425 limits levels of mixing between breeding and non-breeding bats, due to costs such as suboptimal  
426 thermoregulatory conditions, high parasite load, and increased competition. These long-term,  
427 comparative data provided by our study have contributed to the growing base of knowledge on  
428 segregation in bats, e.g. (Altringham *et al.*, 2005; Senior *et al.*, 2005), providing valuable  
429 insights into the mechanisms of segregation patterns.

430

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615 **Figure Legends**

616 **Figure 1.** Patterns of segregation between females of different breeding status, males, and  
617 juveniles (FoNB = failed or non-breeding female, BF = breeding female, M = male, J =  
618 juvenile) across the pre-parturition (PP), lactation (L), and post lactation (PL) periods. The  
619 SSAS indicates significant segregation if the observed value (circular point) falls above the  
620 SSAS expected interval (shaded area), aggregation if it falls below the shaded area, and  
621 random association if it falls within the shaded area.

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623 **Figure 2.** Interaction plot displaying the interaction between species and reproductive period  
624 (the pre-parturition (PP), lactation (L), and post lactation (PL) periods), with mean maternity  
625 group size as a response variable.

626

627 **Figure 3.** Fitted beta regression model for a) proportion of males in maternity groups as  
628 response variable and maternity group size as fixed effect, and b) proportion of non-breeding  
629 females in maternity group as response variable and maternity group size as fixed effect.

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642 **Tables**

Site code	Approximate size (ha)	Box types	Species monitored
a	400	Schwegler™ 2M Schwegler™ 1B	<i>M. nattereri</i> <i>P. auritus</i>
b	46	Schwegler™ 2FN Schwegler™ 1FW	<i>M. bechsteinii</i>
c	47	Schwegler™ 1FF Schwegler™ 1FS Schwegler™ 2F Schwegler™ 2FN	<i>M. nattereri</i> <i>P. auritus</i>
d	91	Schwegler™ 1FF Schwegler™ 2F Schwegler™ 2FN Home-made woodcrete	<i>M. bechsteinii</i> <i>P. auritus</i>
e	28	Schwegler™ 1FF Schwegler™ 1FD Schwegler™ 1FS Schwegler™ 2F Schwegler™ 2FN	<i>M. nattereri</i> <i>P. auritus</i>
f	1	Unknown	<i>M. bechsteinii</i> <i>P. auritus</i>
g	59	Schwegler™ 1FF Schwegler™ 1FS Schwegler™ 2F Schwegler™ 2FN	<i>M. nattereri</i> <i>P. auritus</i>
h	17	Schwegler™ 2FN	<i>M. bechsteinii</i>

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644 **Table 1.** Site information from anonymized bat monitoring schemes in S.W. England,

645 including species monitored, approximate area of woodland site, and artificial roost types.

646 Box types ranged 26-44 cm in height. All Schwegler™ boxes had a round base ranging 12-28

647 cm in diameter, apart from the square Schwegler™ 1FF, which had a depth of 14 cm. Only

648 species that are relevant to this study are included among species monitored for each site.

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<b>Species</b>	<b><i>M. bechsteinii</i></b>	<b><i>M. nattereri</i></b>	<b><i>P. auritus</i></b>
No. roosts	323	484	188
No. detections adult males	124	427	234
No. detections breeding females	1126	1552	360
No. detections failed or non-breeding females	711	651	115
No. detections juvenile males	519	537	123
No. detections juvenile females	487	482	118

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653 **Table 2.** Collated data included in SSAS analysis.

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Random effects	Variance	Standard deviation	
Individual ID (intercept)	0.120	0.346	
Year	0.136	0.368	
Residual	0.174	0.417	
Fixed effects	Estimate	Standard error	P value
Intercept	8.72	0.115	< 0.001 ***
<i>M. nattereri</i>	-0.888	0.100	< 0.001 ***
<i>P. auritus</i>	-0.829	0.104	< 0.001 ***
Male	-0.404	0.0364	< 0.001 ***
Non-breeding	-0.115	0.0638	0.0710
Post-lactating	0.209	0.0644	0.00121 **
Pregnant	1.05	0.0733	< 0.001 ***

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**Table 3.** Results of linear mixed effects model with body weight as a response, and fixed effects including species, sex, and reproductive status, and a random intercept effects of individual ID and year.

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Fixed effects	Estimate	Standard error	P value
Intercept	3.00	0.0296	< 0.001 ***
<i>M. nattereri</i>	-0.650	0.0380	< 0.001 **
<i>P. auritus</i>	-0.595	0.0637	< 0.001 ***
Post lactation period	-0.425	0.0390	< 0.001 ***
Pre-parturition period	-0.795	0.0453	< 0.001 ***
Post lactation: <i>M. nattereri</i>	-0.0530	0.0589	0.368
Pre-parturition: <i>M. nattereri</i>	0.534	0.0644	< 0.001 ***
Post lactation: <i>P. auritus</i>	0.190	0.100	0.0591
Pre-parturition: <i>P. auritus</i>	0.329	0.0908	< 0.001 ***

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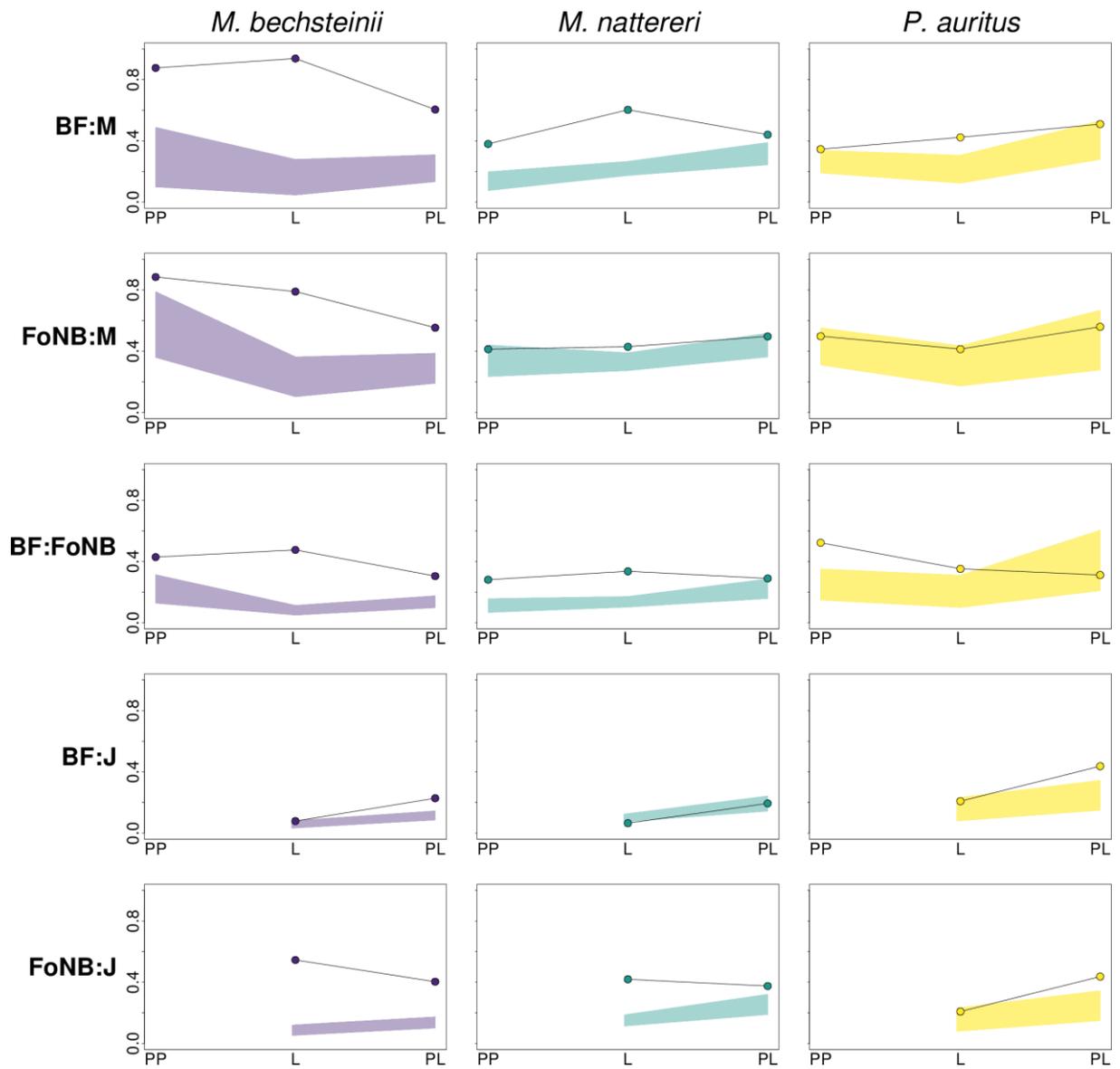
**Table 4.** Results of generalized linear model with a Poisson error distribution and group size

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as a response variable. Fixed effects included species and reproductive period, and an

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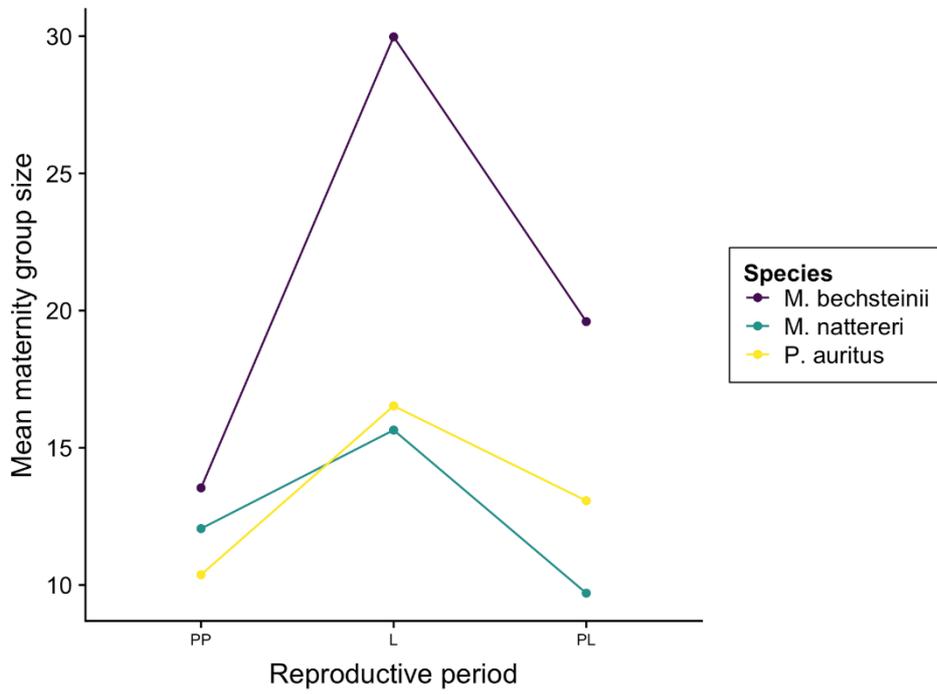
interaction effect of species and period.



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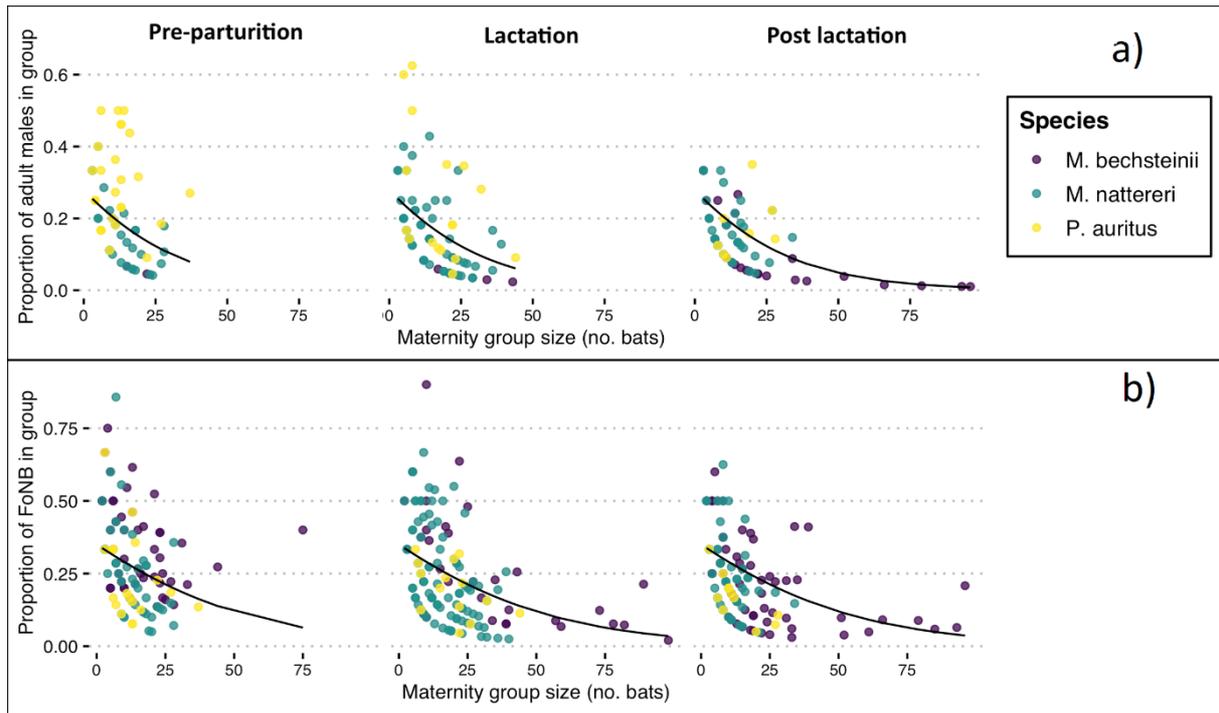
Figure 1

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Figure 2



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Figure 3