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1 **Interspecific competition between two partridges in farmland landscapes**

2

3 Tony Rinaud*¹, Clément Harmange*^{1,2}, Olivier Pays², Mathieu Sarasa^{3,4},

4 Maxime Saillard¹ and Vincent Bretagnolle^{1,5}

5

6 ¹*Centre d'Etudes Biologiques de Chizé, UMR 7372, CNRS and Université La Rochelle, F-79360*

7 *Beauvoir-sur-Niort, France*

8 ²*LETG-Angers, UMR 6554 CNRS, Université d'Angers, 49000 Angers, France*

9 ³*BEOPS, 1 Esplanade Compans Caffarelli, 31000 Toulouse, France (current address)*

10 ⁴*Fédération Nationale des Chasseurs, 13 rue du Général Leclerc, 92136 Issy-les-Moulineaux*

11 *cedex, France (former address)*

12 ⁵*LTSE « Zone Atelier Plaine & Val de Sèvre », CNRS, 79360, Beauvoir sur Niort, France*

13 **Co-first authors*

14 Corresponding author:

15 Clément Harmange, *LETG-Angers, UMR 6554 CNRS, Université d'Angers, 49000 Angers,*

16 *France, +33671918570, clement.harmange@orange.fr*

17

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Interspecific competition between two partridges in farmland landscapes

ABSTRACT

Interspecific competition is expected to occur between phylogenetically closely related species when sharing resources. In birds, interspecific competition often occurs by song-mediated interference, and frequently implies asymmetrical outcomes between the species-pairs involved. Habitat loss resulting from agricultural intensification is expected to have aggregated bird species in the remaining suitable habitats, thus increasing the likelihood of interspecific competition. However, this process has rarely been considered as a potential factor limiting population recovery in farmland birds. We investigated whether interspecific competition occurs between grey (*Perdix perdix* L. 1758) and red-legged (*Alectoris rufa* L. 1758) partridges, two phylogenetically related species. Originally parapatric, they have suffered an artificial increase in their contact zone due to huge human-mediated gamebird releases. We analyzed territorial behaviour through a playback stimuli experiment and investigated shifts in habitat niche in absence and presence of a hypothetical competitor. Results showed that the grey partridge appeared less territorial when co-occurring with the red-legged partridge and shifts its habitat niche away from that occupied by the red-legged partridge, while no such change was detected for the red-legged partridge. These asymmetrical patterns in behaviour and ecology are predicted under an interspecific competition scenario beneficial to the red-legged partridge, and therefore suggest that red-legged partridges are competitively dominant to grey partridges where they co-occur. This result has potentially strong implications for the management of grey partridges as gamebirds, and for their conservation in areas where they are almost extirpated.

25 **Key words**

26 Asymmetric competition, Grey partridge, Habitat niche displacement, Playback experiment,

27 Red-legged partridge, Territorial behaviour.

28

29

30 INTRODUCTION

31 Interspecific competition is a major driver of trophic interactions (MacArthur & Levins,
32 1964), and may define ecological niches (Diamond, 1978; Martin & Martin, 2001b),
33 determine biogeographic patterns (Bull, 1991; Jankowski et al., 2010) and affect
34 evolutionary processes (Svårdson, 1949; Wiens, 1992). Interspecific competition is expected
35 to occur between phylogenetically close species sharing limiting resources (Wiens, 1992),
36 either indirectly through resource depletion (Dhondt, 2012; Schoener, 1983), or directly
37 through agonistic interactions (Persson, 1985; Wiens, 1992). Agonistic interactions are in
38 most cases asymmetric in vertebrates (Martin et al., 2017; Pasch et al., 2013; Persson, 1985;
39 Schoener, 1983): in an analysis of phylogenetically close bird species, 224 out of 270 species-
40 pairs showed asymmetric agonistic interactions, benefiting the larger species in 87% of the
41 cases (Martin et al., 2017). Typically, larger and dominant species show little difference in
42 territorial response (vocal behaviour and approaches) to heterospecific versus conspecific
43 songs, while smaller (subordinate) species show lower response rates to the heterospecific
44 versus conspecific song (Martin & Martin, 2001a; McEntee, 2014). This may result in a shift
45 in the song schedule to avoid territorial interaction (Brumm, 2006; Cody & Brown, 1969) and
46 in the displacement and/or contraction of the ecological niche of the subordinate species
47 (Jankowski et al., 2010; Martin & Martin, 2001b; Svårdson, 1949; Tarjuelo et al., 2017). Such
48 asymmetric outcomes may impact population dynamics of subordinate species, by
49 constraining its distribution to lower quality habitats, resulting in lower breeding success
50 and/or survival (Martin et al., 2017; Martin & Martin, 2001b).

51 Recent declines in rural landscape habitat quality, the result of post-war changes in
52 agricultural practices, has not only triggered a decline in European farmland birds (Benton et
53 al., 2003; Newton, 2004; Robinson & Sutherland, 2002), but has also aggregated surviving

54 bird populations into the remaining local patches of suitable habitat (Aebischer & Ewald,
55 2012). While an increasing likelihood of interspecific competition should be expected in
56 those habitats (Newton, 2004; Robillard et al., 2013), the implications for farmland bird
57 decline or population recovery limitation has remained largely unexplored (though see
58 Robillard et al., 2013). The grey partridge *Perdix perdix* L. 1758 and red-legged partridge
59 *Alectoris rufa* L. 1758 are phylogenetically related and belong to the Phasianidae (Wang et
60 al., 2013). They were originally parapatric, showing separated but contiguous distributions
61 (Cramp & Simmons, 1980; see also Watson, 1962; Bull, 1991), with the grey originating from
62 central Europe and Asia (Liukkonen-Anttila et al., 2002) and the red-legged from Iberia
63 (Ferrero et al., 2011). Originally, the distributional contact zone was primarily restricted to
64 central and southern France and north-west Italy (Cramp & Simmons, 1980). However, huge
65 releases of red-legged partridges as gamebirds in the UK and France (Aebischer, 2019;
66 Cramp & Simmons, 1980) resulted in the current situation where both species are sympatric
67 over vast areas of western Europe. Both species select open agricultural landscapes
68 (Aebischer & Kavanagh, 1997; Aebischer & Lucio, 1997; Potts, 1980), have similar breeding
69 habitats (Bro et al., 2013; Green et al., 1987; Rands, 1988), though slight differences in
70 micro-habitat exist (Meriggi et al., 1991). They also overlap in their breeding phenology (egg
71 laying in May-June, peak of territorial activity in February-April; Rotella & Ratti, 1988). In
72 addition, chicks feed on the same arthropod taxa, while adults shift to leaves and seeds (Bro
73 & Ponce-Boutin, 2004; Green, 1984; Green et al., 1987). Finally, partridges are highly
74 territorial, with both mates contributing to territory defense (Casas et al., 2016; Potts, 1980).
75 The original narrow contact zone between both species was suggestive of the presence of
76 competition interactions (Bull, 1991; Watson, 1962). These can now expected to be present

77 over the entire, vast, contact zone (Jankowski et al., 2010; Martin & Martin, 2001a; McEntee,
78 2014).

79 The possible increased competition pressure from the introduction of the larger and
80 bulkier red-legged partridge in the human-created contact zone (Carpio et al., 2017;
81 Robertson, 1996; Sokos et al., 2008), has rarely been studied as a possible cause of grey
82 partridge decline or as a limiting factor in population recovery (Bro, 2016; Meriggi et al.,
83 1991). However, while the grey partridge is one the most iconic farmland bird in Europe
84 (Sotherton et al., 2014), it has declined strongly over the last few decades (Aebischer &
85 Kavanagh, 1997; Aebischer & Potts, 1994) and is now threatened at national or sub-national
86 scales (Charra & Sarasa, 2018; Eaton et al., 2015). In this study, we investigated behaviours
87 that might potentially indicate interspecific competition between the two partridges, in
88 study areas located within the original area of sympatry (central western France). We
89 quantified territorial behaviour through playback stimuli, analyzing the patterns of territorial
90 response in single- and two-species situations (Cody & Brown, 1969; Martin & Martin,
91 2001a), and further investigated behavioural (territorial daily activity) and habitat niche
92 shifts in the area of co-occurrence. Based on the asymmetric interspecific competition
93 hypothesis, we predicted that grey partridge (smaller species) should respond less to red-
94 legged partridge than to the conspecific call both in the absence and co-occurrence of red-
95 legged partridge, and should show lower levels of agonistic behaviour in co-occurrence
96 areas. Conversely, red-legged partridge should increase its territorial response to grey
97 partridge in co-occurrence situations, while maintaining or increasing its agonistic behaviour.
98 We also predicted that grey partridge should restrict their daily activity pattern when co-
99 occurring with red-legged partridge to minimize inter-specific encounters. Finally, habitat
100 niche of the putatively subordinate grey partridge should shift when in co-occurrence with

101 red-legged partridges, while the putatively dominant red-legged partridge should be
102 unaffected by the presence of grey partridge.

103

104 **MATERIAL & METHODS**

105 *Study area*

106 The study was conducted in the Long-Term Socio-Ecological Research platform (LTSER)
107 “Zone Atelier Plaine & Val de Sèvre” (hereafter, ZAPVS), Central Western France, (Fig. 1 ;
108 Bretagnolle et al., 2018b), in 2016 and 2017. This is a 435 km² zone of intensive agricultural
109 cultivation, comprising winter cereals (41.5%), sunflower (10.4%), maize (9.6%), rape (8.3%),
110 meadows (13.5%), woodlands (2.9%) and built-up areas (9.8% ; average values 2009-2016 in
111 Bretagnolle et al., 2018b). Within the ZAPVS, a restricted study site of 34 km² (2016) to 68
112 km² (2017) was chosen where both partridge species were historically the most observed
113 during the past two decades (Fig. 1). In 2017, a second study site, with higher partridge
114 densities than the ZAPVS, was added to increase the sightings dataset (Table A1, Appendix
115 A). To maintain homogeneity in birds’ phenology, this second site is located close to the
116 ZAPVS and has similar habitat types. This 18 km² site is located in the south of Maine-et-
117 Loire (METL; Fig. 1).

118

119 *Survey protocol and playback tests*

120 We first established a grid of playback stations with a cell size of 500 m (excluding built-up
121 areas) to locate territorial pairs accurately (the size of a single home range is about 20 ha in
122 spring-summer: Birkan et al., 1992). Sample points were placed as close as possible to the
123 centroid of the grid cells, but still on a path or a road for ease of access and minimize
124 disturbance. Each sample point was surveyed four times per year, with two sessions in the

125 morning and two in the evening, as patterns of daily vocal activity peak at dawn and dusk
126 (Pépin & Fouquet, 1992). Sample points were slowly approached by car, the observer then
127 went out quietly and waited for 1 minute before starting a session. A session consisted of
128 broadcasting, at fixed volume (calibrated to be heard up to 250 meters away to avoid
129 overlap between neighboring points) with a NEWONLINE N74® speaker, of an audio
130 sequence containing territorial calls of males of both study species (155 seconds for each
131 species), and of the common quail *Coturnix coturnix* L. 1758 call as control. For each species,
132 bouts were separated by 1-min silence (see Appendix B for more details about sequence
133 preparation and call origins). Since calls of three species were broadcast, six audio sequences
134 containing the six possible broadcasting combinations were prepared and one of them was
135 randomly played at each session. In 2016, surveys were conducted at 140 playback stations
136 at ZAPVS (April 6 to April 25), while in 2017, 275 stations were surveyed at ZAPVS and 75 at
137 METL, from March 14 to April 28. Surveys involved tracks of 14-17 sampling points along a
138 road/path, with each track corresponding to a sequence of points made in the morning or
139 evening session. Tracks were made alternately in a way, then in the other, to avoid hourly
140 biases in the sequence of points.

141 For each point in a given year, we determined whether none, one or the two species
142 were present, if contacted at least once over the four sampling sessions. Points were then
143 classified into four distinct categories as to whether none, only one or both partridges were
144 contacted. The “no contact” category was discarded, so that only points with at least one
145 occurrence were kept for analyses, assuming that a species was absent of a point if no
146 sighting was recorded there across the four sampling sessions. We checked whether
147 discarded points might actually contain partridges using rarefaction curve analyses (see
148 Appendix C): only 7.3% and 12.5% of points for grey and red-legged partridges, respectively,

149 may have been removed erroneously. For each individual contacted at a point, we noted the
150 playback call that elicited the response, the type of response (0: no response, 1: response to
151 one of the partridge species calls, 2: response to both partridge stimuli), the latency of
152 response (elapsed time between the beginning of the playback and any territorial response)
153 and territorial behaviour (walking approach, flight approach, calling).

154

155 *Ecological habitat description*

156 Analysis was based on three datasets of grey and red-legged partridge occurrence collected
157 by fieldworkers at ZAPVS between 2013 and 2017 (see Harmange et al., 2019). The first
158 dataset contained occurrences from systematic bird point counts without playback (see
159 Brodier et al., 2014 for protocols), and sampled some 450 points spread throughout the
160 ZAPVS each year during the passerine breeding period (Bretagnolle et al., 2018a). The
161 second dataset comprised of opportunistic sightings made when fieldworkers saw partridges
162 while studying other bird species (Bretagnolle et al., 2018b), or during the systematic land
163 cover monitoring performed twice a year over the entire study site (see Harmange et al.,
164 2019). Each year, opportunistic monitoring occurred daily from late March to late July. The
165 third dataset contained partridge sightings from the playback experiment (see above).
166 Collating the three datasets, a total of 286 and 244 locations had grey and red-legged
167 partridges, respectively.

168 From the annually collected land cover data, we then created a grid of 600 x 600 m²
169 cells, using R (R Core Team, 2017) and QGIS (Quantum GIS Development Team, 2017),
170 excluding all pixels that had less than half their area (18 ha) lying within the study site. Pixel
171 size was chosen as the minimal size that contained sufficient numbers of pixels with (i) only
172 grey partridge occurrences over the period 2013-2017 (n = 115), (ii) only red-legged

173 partridge occurrences (n = 137), or (iii) both partridge species (n = 32). Analyzed landscape
174 metrics were based on those identified as being selected (either positively or negatively) in
175 grey and/or red-legged partridges (Birkan et al., 1992; Bro et al., 2013; Harmange et al.,
176 2019; Meriggi et al., 1991; Rands, 1987): cereals, rape, meadows, spring crops (corn,
177 sunflower etc.), hedgerows, roads/tracks, woodlands and buildings. Landscape metrics used
178 in analyses corresponded to the surface area (or total length in m) of each habitat had in the
179 pixel, divided by the pixel surface area (to account for edge effect). Each parameter was
180 calculated annually from 2013 to 2017, except for roads and hedgerows, which remained
181 stable and for which we set only one layer (Harmange et al., 2019).

182

183 *Ethical note*

184 This study is restricted to behavioural observations of partridges and, therefore, excludes
185 any animal handling or invasive experiments. Field studies did not involve endangered or
186 protected species. Farmers were made aware of the study, which did not involve any
187 penetration to private properties. The study thus adheres to the “Guidelines for the Use of
188 Animals in Research”, and to the legal requirements of the country in which the work has
189 been carried out. Our project was conducted with clearance from the authority *Préfecture*
190 *Départementale des Deux-Sèvres* (Number: 2017/1).

191

192 *Statistical analyses*

193 *Territorial behaviour*

194 GLMMs (binomial response variable, logit link) were used to investigate presence/absence of
195 each species’ territorial response (vocalization and/or approach) using the *lme4* R package
196 (Bates et al., 2018), as a function of the interaction between playback stimuli (*broadcast*

197 *species*) and the *interspecific situation* (target species *alone* or in *co-occurrence* with the
198 other species). The *playback sequence* (6 levels) and the *rank* of partridge call (1st or 2nd
199 position) were considered as random factors. When needed, Tukey's multiple comparison
200 tests were performed using with the R package *emmeans* (Lenth et al., 2019). For each
201 species, we further analyzed the magnitude of territorial response, described by four
202 parameters calculated for each point count station. These included *territorial response rate*
203 (number of responding individuals within pairs, 0/1/2), *response latency* (in seconds), *calling*
204 *behaviour* (0: no response, 1: response to one of the two partridge species calls, 2: response
205 to both partridge stimuli), and a *territoriality score* in the form of a ranking of increasing
206 territorial behaviour intensity (0: no response, 1: approach, 2: vocalization, 3: approach with
207 vocalization, 4: flying approach with vocalization; see Table A2 in Appendix A for more
208 details about variables calculation). Then, for each species, we carried out linear discriminant
209 analyses (LDA) (James & McCulloch, 1990) to investigate whether territorial behaviour
210 (described from the four behavioural variables) allowed discrimination between the two
211 interspecific situations, i.e. when a single species was observed and when both species co-
212 occurred. LDA allowed the difference between two situations (alone or co-occurrence) to be
213 maximized statistically for each species using a discriminant function assessed from four
214 observed territorial behaviours. This analysis was performed using the *MASS* R package
215 (Ripley, 2017). To handle the differences in sample sizes between the two situations (alone
216 or co-occurrence) given the low sample size of the "co-occurrence" category, we produced
217 95% confidence intervals (CI) for linear discriminant scores following Luttrell & Lohr (2018).
218 CI was assessed by generating bootstrap samples with replacement and simulating 1000 sets
219 for the "alone" category (highest sample size) with reduced sample size equal to the smaller
220 "co-occurrence" set. The mean of the linear discriminant scores +/- SD for each of the 1000

221 bootstrapped samples was calculated and a 95% CI was computed for the “alone” category.
222 Finally, we carried out analyses of variance (ANOVA) to test whether each territorial
223 behaviour (see above) contributes significantly to discriminate the two interspecific
224 situations (species alone vs co-occurrence).

225 To investigate the daily pattern of territorial behaviour for each species, we first
226 summed the number of territorial responses (vocal behaviour and approaches) for a 30-
227 minute period, using four categories: grey partridge alone and grey co-occurring with red-
228 legged partridge, and red-legged partridge alone and red-legged co-occurring with grey
229 partridge. The sum (per half-hour) was then standardised (divided) by the number of trials
230 performed on that given 30-minute period. Seasonal effects were controlled for by
231 considering time (GMT) relative to sunrise (for sampling points in the morning) or sunset
232 (evening). To compare the distribution of territorial responses across the four modalities, we
233 performed Cramér-von Mises distribution tests (Anderson, 1962; Conover, 1999), using the
234 *RVAidememoire* R package (Hervé, 2018).

235

236 *Habitat niche modelling*

237 Within-species habitat niches were analyzed with data from 2013-2017, averaging
238 environmental layers across years for each pixel. Three types of occurrences (2013-2017)
239 were considered: (1) occurrence of grey partridge only (at least once) in the pixel over the 5
240 years (n = 222); (2) occurrence of red-legged partridge only (n = 192); (3) grey (n = 64) and
241 red-legged (n = 52) partridges co-occurring, each being recorded at least once (but not
242 necessarily simultaneously). To compare species niches in presence of a single species versus
243 co-occurrence of the two species, we used Broennimann et al. (2012)'s niche modelling
244 framework implemented in the *ecospat* R package (Broennimann et al., 2016). The first step

245 consists of describing the environmental space available in the study area, using the first two
246 axes of a principal component analysis (PCA-env) performed on all pixels, with each
247 environmental layer being a different variable in the PCA. Then, for each species in each
248 situation (species alone or in co-occurrence), a smoothed density of occurrences in the PCA-
249 env space is obtained using a kernel density function. This allows niche space to be
250 graphically delineated, for each situation, as a relative abundance index ranging from 0
251 (environmental conditions in which the species was not observed) to 1 (environmental
252 conditions in which the species was most commonly observed), thus handling between-
253 group differences in the number of occurrences. Niche overlap can then be calculated (e.g.
254 between grey alone and grey co-occurring with red-legged partridge), using Schoener's D
255 index (Warren et al., 2008) which ranges from 0 (no overlap) to 1 (full overlap). The niche
256 equivalency test, a commonly-used niche randomization test, was performed (Broennimann
257 et al., 2012; Warren et al., 2008). In this test, the two occurrence datasets are mixed, and
258 two new datasets are reconstituted randomly (1000 times), conserving the sizes of the two
259 original datasets. The distribution of the 1000 D niche overlap values from the paired
260 simulated datasets are then compared with the observed value of D: if the latter is outside
261 the 95% range for the simulated values, the null hypothesis is rejected, i.e. the observed
262 niches are less equivalent than expected by chance (Broennimann et al., 2012; Warren et al.,
263 2008). All statistical analyzes were performed using R software (R Core Team, 2017).

264

265 **RESULTS**

266 *Territorial behaviour*

267 Among the surveyed points (combining both study sites), there were 21 and 106 points
268 (respectively 2016 and 2017) with at least one species in one of the four sampling sessions.

269 Assuming that the presence of an individual in at least one sampling session for a given point
270 count reflected the presence of a territorial pair, 37 points (7.5%) with grey partridge, 74
271 (15.1%) with red-legged partridge and 16 (3.3%) with both species were recorded. We found
272 that grey partridge territorial responses were significantly influenced both by the broadcast
273 species and whether red-legged partridge co-occurred (Table 1): they responded more to
274 the conspecific than heterospecific call or to the control call (Fig; 2a, Table A3), but co-
275 occurrence with red-legged partridge significantly reduced grey partridge response (Fig. 2a,
276 Table A3). Similarly, territorial responses of red-legged partridge, when alone, were higher to
277 the conspecific call than the grey partridge or control call (Fig. 2b, Tables 1, A3). Unlike the
278 grey partridge, the red-legged demonstrated a balanced response whichever the species
279 when co-occurring with grey partridge (Fig. 2b, Table A3).

280 Scores of territorial behaviour in response to playback (from the four behavioural
281 variables) allowed discrimination between situations when grey partridges were alone or co-
282 occurring with red-legged partridges. Territorial response rate, calling behaviour and
283 territoriality score were the three highest contributing variables discriminating territorial
284 behaviour between the two situations (Fig. 3b). In situations of co-occurrence the grey
285 partridge reduced its response rate, number of calls and intensity of territorial response (i.e.
286 territorial score) significantly (ANOVA, Table A4). These results suggest a shift in the
287 territorial behaviour of the grey partridge in co-occurrence situations (Fig. 3a). Conversely,
288 behavioural variables were very poor contributors in discriminating situations where red-
289 legged were alone or co-occurring with grey partridges (Fig. 3d). Indeed, no significant
290 differences appeared for any of the four behavioural variables in the red-legged partridge
291 responses (ANOVA, Table A4), indicating no shift in behaviour similar to that found for the
292 grey partridge (Fig. 3c).

293 Daily pattern of grey partridge territorial behaviour was significantly affected by co-
294 occurrence with red-legged partridge (Fig. 4, Table A5, Appendix A): under co-occurrence,
295 grey partridge territorial response became concentrated around the sunset in the evening,
296 while no changes were detected in the morning (Fig. 4). A similar pattern was detected for
297 the red-legged partridge where alone versus in co-occurrence with the grey partridge (Fig. 4,
298 Table A5).

299

300 *Habitat niche*

301 Analysis showed that the grey partridge's habitat niches when alone or when co-occurring
302 with the red-legged partridge overlapped by only 53%. The equivalency test was significant
303 ($p = 0.02$), indicating that the grey partridge habitat niche significantly shifted in the
304 presence of the red-legged partridge. Although the Figure 5 suggests a moderate shift (Fig.
305 5a compared to 5b), the core of the grey partridge's habitat niche changed in the opposite
306 direction of the red-legged partridge's habitat niche, towards greater proportions of spring
307 crop, cereal and rape habitats, and lower proportions of meadows and hedgerows (Fig. 5e).
308 Overall, the red-legged partridge's habitat niche was wider, comprised of its preferred open
309 arable land (e.g. spring crops, cereals and rape) associated with semi-natural permanent
310 covers (meadows and hedgerows), but the species also avoided closed habitats (woodlands
311 and built-up areas, Fig. 5e). In contrast to the grey partridge, the red-legged partridge's
312 habitat niches when alone or when co-occurring with the grey partridge showed more
313 overlap (67%, Fig. 5c, d). When co-occurring with the grey partridge, the red-legged's habitat
314 niche did not shift, so remaining equivalent in both situations (equivalency test, $p = 0.55$).

315

316 **DISCUSSION**

317 As expected, our results suggest an asymmetric pattern of territorial behaviour between
318 grey and red-legged partridges. Grey partridges reduced their territorial response, and
319 shifted both their hourly territorial behaviour and their habitat niche when co-occurring with
320 the red-legged partridge.

321 Such shifts in territorial behaviour intensity towards a more discreet behaviour when
322 facing a competitive species have been documented previously in birds (e.g. Martin &
323 Martin, 2001a; McEntee, 2014) and other vertebrates, such as mammals (e.g. Pasch et al.,
324 2013). Indeed, in such cases, the typical response of the subordinate species is to avoid
325 unfriendly interactions with a dominant and larger competitor. Conversely, the red-legged
326 partridge territorial response rate showed much higher response rate to its own species
327 when alone, but shifted to balanced response rates to both species in situations of co-
328 occurrence. Such convergence of territorial behaviour has already been documented for
329 dominant species involved in asymmetric interspecific interactions (Jankowski et al., 2010;
330 Pasch et al., 2013) and reject the hypothesis of Murray (1971), which suggests that
331 interspecific territoriality results from misdirected intraspecific interactions due to incorrect
332 signal recognition. However, huge releases of captive-reared partridges for game
333 management could alternatively explain responses to heterospecific call, as both partridge
334 species are often reared in the same farms and may have been sensitized or conditioned by
335 a precocious exposure to the heterospecific call. We suggest that this alternative hypothesis
336 is however unlikely because under the hypothesis of a precocious sensitization in rearing
337 farms, both species should have responded to heterospecific calls (not just to the red-legged
338 partridge), and additionally, each species should have responded to the heterospecific
339 stimuli, whether in absence of competitors or in co-occurring situations. In addition, we
340 found that both species adjusted their daily territorial activity under co-occurrence, though

341 territorial activity of both species remained synchronized, while a temporal segregation was
342 expected. This may be the result of a too coarse temporal resolution in our analyses, making
343 temporal shifts in territorial response hard to detect. For instance, Brumm (2006) showed
344 the temporal segregation in territorial activity occurs at a finer scale in Nightingale *Luscinia*
345 *meigarhynchos*, which adjusts and focuses its vocal activity within the silent intervals
346 between two heterospecific broadcast songs (see also Cody & Brown, 1969). An alternative
347 explanation would be that given the calls of both partridges are acoustically different, this
348 might have enabled vocal activity to remain synchronized, while ensuring a low interspecific
349 interference (Dhondt, 2012; Doutrelant & Lambrechts, 2001).

350 Finally, we detected a slight habitat niche shift in the less competitive species in
351 situations of co-occurrence with the dominant one, while there was no such shift for the
352 dominant species. This pattern is typical of asymmetric competition for habitat likely
353 resulting from the agonistic behaviour of the dominant species (Jankowski et al., 2010;
354 Martin & Martin, 2001a, 2001b). While the grey partridge (subordinate species) selects
355 preferentially grass along hedgerows to nest (Potts & Aebischer, 1991), its habitat niche
356 shifted to more open habitats (more annual crops and less hedgerows) in co-occurrence
357 situations with the red-legged. These habitats that are more subject to human disturbance,
358 may therefore be of poorer-quality for breeding (Burel et al., 1998), likely resulting in lower
359 fitness and/or survival (see Martin et al., 2017; Martin & Martin, 2001a, 2001b). Such habitat
360 niche shift, likely resulting from interspecific competition, could have also driven the micro-
361 habitat segregation observed by Meriggi et al. (1991), with the grey partridge being
362 generally more associated with crops and open lands, while the red-legged is more linked to
363 semi-natural elements like hedgerows.

364 Asymmetric competition occurring in the contact zone of parapatric species is well-
365 known to reduce fitness of the subordinate species (Jankowski et al., 2010; Martin & Martin,
366 2001a). Such behavioural outcomes of competition may have strong implications for the
367 conservation and management of partridges. Although releasing non-native species has long
368 been used as a strategy to limit hunting pressure on wild native populations (Aebischer &
369 Ewald, 2004; Bro, 2016; Carpio et al., 2017), the huge releases of red-legged partridges in the
370 core area of the grey partridge raise concerns not only for the grey partridge decline, but
371 also for its future possible recovery. The presence of morphologically similar species has long
372 been identified as interfering with the re-establishment success in translocations (Griffith et
373 al., 1989). The grey partridge is currently a focus of interest for many reinforcement projects,
374 that are identified as the only tool for restoring self-sustaining populations in many areas
375 (Buner et al., 2011; Buner & Aebischer, 2008). However, this has proved inefficient or even
376 counterproductive (Reitz, 2003; Sokos et al., 2008), because of many unintentional but
377 adverse effects on population dynamics (inadvertent shots: in Aebischer & Ewald, 2004;
378 parasite-mediated competition: in Tompkins, Greenman, et al., 2000; Tompkins, Draycott, et
379 al., 2000). Our results suggest further impacts on territorial behaviour and access to
380 resources for the native species, though the effects on demography remain unexplored. Our
381 study thus suggests that the presence of red-legged partridges may limit the chances of
382 success in such projects. Therefore, to quantify the strength of competitive interaction
383 effects on population dynamics, further field experiments are required to formally conclude
384 that interspecific competition occurs between these species. These should include (i)
385 controlling for the origin of birds (natural or captive birds reared in monospecific farms
386 preventing any early contact between both species), (ii) treatments (deliberately releasing
387 grey partridge only, red-legged only or both species together, in different sites offering the

388 same availability in environmental conditions) and (iii) assessing the influence of species co-
389 occurrence on demographic parameters (adult survival, nest predation, chick survival, see
390 Martin & Martin, 2001b).

391

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610

611 **Table 1** Results of GLMMs (binomial, logit) considering the territorial response (vocal behaviour and /
 612 or approaches) of grey and red-legged partridges as response variable.
 613

Species	Variable	χ^2 - value	df	P-value	Estimate \pm SE	Variance of random effects
Grey partridge					(intercept: -2.867 ± 0.413)	<i>Sequence</i> : <0.001 <i>Rank</i> : 0.146
	Broadcast species x interspecific situation	1.455	2	0.483		
	Broadcast species	38.023	2	<0.001	(see Table A3 for multiple comparisons)	
	Interspecific situation	6.942	1	0.008	Co-occurrence: -0.691 ± 0.272	
Red-legged partridge					(intercept: -2.736 ± 0.476)	<i>Sequence</i> : 0.041 <i>Rank</i> : 0.085
	Broadcast species x interspecific situation	8.060	2	0.018	(see Table A3)	
	Broadcast species	19.352	2	<0.001	(see Table A3)	
	Interspecific situation	0.258	1	0.611		

614 *Explanatory variables are the broadcast species (control, grey partridge, red-legged partridge) and*
 615 *the interspecific situation (Alone, Co-occurrence). Modalities in italics are considered as references. All*
 616 *models include the playback sequence (n=6) and the rank (n=2) of the partridge broadcast calls (grey*
 617 *partridge or red-legged partridge broadcast first) as random effect.*
 618
 619

620 **Table A1** Grey and red-legged partridge density estimations (mean \pm SD) in the Long-Term Socio-
 621 Ecological Research site “Zone Atelier Plaine & Val de Sèvre” (LTSER ZAPVS) and the Maine-et-Loire
 622 study area (METL) in 2017.

Species	Density in the LTSER ZAPVS	Density in the METL study area
Grey partridge	0.25 (\pm 0.07)	0.49 (\pm 0.20)
Red-legged partridge	0.15 (\pm 0.09)	2.62 (\pm 0.54)

623
 624 *Estimations were derived from playback experiments of 2016 and 2017.*

625
 626
 627 **Table A2** Description of behavioural variables considered in the analysis of territorial behaviour, and
 628 predictions under a hypothetic asymmetric competition for the dominant and subordinate species.
 629

Behavioural metric	Description	Prediction
Territorial response intensity	The sum of responding individuals (by approach and or vocalization) controlled by the number of expected responses (number of individuals seen on this point)	In co-occurrence areas, we expected a higher territorial response intensity for the dominant species, and a lower response intensity for the subordinate one (see Jankowski et al., 2010; Martin & Martin, 2001a)
Response latency	The mean response latency (i.e. the time spent between the beginning of the broadcast call and the vocal response) recorded over the 4 sampling sessions	In co-occurrence area, the response latency is expected to be lower for the dominant species, higher for the subordinate (see Jankowski et al., 2010; Martin & Martin, 2001a)
Calling behaviour	The mean number of calls responded to by individuals, between the conspecific and heterospecific partridge calls. Ranges from 0 (no individual responded to partridge calls over the four sampling sessions), to 2 (all individuals responded to the two partridge calls during each of the four sessions)	Expected to be high for a dominant species responding as well as conspecific than heterospecific call, while it is expected to be low for a subordinate species not responding to the heterospecific call (Martin & Martin, 2001a)
Territoriality score	The mean of the territoriality score obtained by each individual across the four sampling sessions, following the ranking of increasing territoriality: 0 – no response, 1 – approach, 2 – vocalization, 3 – approach with vocalization, 4 – flying approach with vocalization	We expected the dominant species to demonstrate a higher territoriality score in co-occurrence with the subordinate one, while the reverse was expected for the subordinate species (see Jankowski et al., 2010; Martin & Martin, 2001a)

630
 631 *Metrics were calculated for each species, from each point count.*

632
 633

634 **Table A3** Tukey's multicomparison post-hoc tests computed after GLMMs (Link = binomial, logit)
635 performed on the territorial response of grey and red-legged partridge species.
636

Species	Variable	Estimate	SE	z-ratio	p-value
Grey partridge	Grey partridge – Red-legged partridge	1.140	0.279	4.084	<0.001
	Grey partridge – Common quail	1.748	0.337	5.192	<0.001
	Red-legged partridge – Common quail	0.608	0.376	1.620	0.234
Red-legged partridge	Red-legged partridge, Alone – Grey partridge, Alone	1.073	0.253	4.245	<0.001
	Red-legged partridge, Alone – Common quail, Alone	0.946	0.244	3.883	0.001
	Red-legged partridge, Alone – Grey partridge, Co-occurrence	0.327	0.339	0.967	0.922
	Red-legged partridge, Alone – Common quail, Co-occurrence	1.091	0.443	2.461	0.125
	Red-legged partridge, Alone – Red-legged partridge, Co-occurrence	0.780	0.394	1.979	0.334
	Red-legged partridge, Co-occurrence – Grey partridge, Alone	0.293	0.425	0.689	0.982
	Red-legged partridge, Co-occurrence – Common quail, Alone	0.166	0.420	0.395	0.999
	Red-legged partridge, Co-occurrence – Grey partridge, Co-occurrence	-0.453	0.480	-0.944	0.929
	Red-legged partridge, Co-occurrence – Common quail, Co-occurrence	0.311	0.559	0.556	0.993
	Grey partridge, Alone – Common quail, Alone	-0.127	0.290	-0.438	0.998
	Grey partridge, Alone – Common quail, Co-occurrence	0.018	0.470	0.038	1.000
	Grey partridge, Alone – Grey partridge, Co-occurrence	-0.746	0.374	-1.994	0.327

Grey partridge, Co-occurrence – Common quail, Alone	0.618	0.368	1.681	0.523
Grey partridge, Co-occurrence – Common quail, Co-occurrence	0.764	0.521	1.466	0.668
Common quail, Alone – Common quail, Co-occurrence	0.145	0.465	0.311	1.000

638 *Variables considered are the broadcast species call (grey partridge, red-legged partridge and common*
639 *quail as control) and the interspecific situation (Alone, Co-occurrence).*

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643 **Table A4** Effect of the independent variable interspecific situation (*Alone*, Co-occurrence) on the
 644 territorial behaviour of grey and red-legged partridges.

Species	Dependent variables	Independent variables	t- value	df	P-value	Estimate ± SE
Grey partridge	Territoriality score	(intercept)	8.013	1	<0.001	(4.270 ± 0.533)
		Interspecific situation	-2.212	1	0.032	Co-occurrence: -2.145 ± 0.970
	Response latency	(intercept)	7.337	1	<0.001	(194.720 ± 26.540)
		Interspecific situation	-0.733	1	0.467	
	Calling behaviour	(intercept)	12.118	1	<0.001	(1.284 ± 0.106)
		Interspecific situation	-2.741	1	0.008	Co-occurrence: -0.529 ± 0.193
	Territorial response rate	(intercept)	14.044	1	<0.001	(0.255 ± 0.018)
		Interspecific situation	-3.098	1	0.003	Co-occurrence: -0.102 ± 0.033
Red-legged partridge	Territoriality score	(intercept)	10.179	1	<0.001	(2.095 ± 0.206)
		Interspecific situation	-0.781	1	0.437	
	Response latency	(intercept)	9.042	1	<0.001	(194.550 ± 21.520)
		Interspecific situation	0.794	1	0.429	
	Calling behaviour	(intercept)	8.966	1	<0.001	(0.718 ± 0.080)
		Interspecific situation	-0.543	1	0.589	
	Territorial response rate	(intercept)	10.900	1	<0.001	(0.174 ± 0.016)
		Interspecific situation	-0.267	1	0.790	

645 *Territorial behaviour was considered as four dependent variables: territoriality score, response*
 646 *latency, calling behaviour and territorial response rate (see Table A2 for more details). The level in*
 647 *italic was considered as the reference in models.*

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 649
 650 **Table A5** Cramer – von Mises' distribution tests comparing the territorial response rates of grey and
 651 red-legged partridges in single-species versus co-occurring situations.

Species	Period	T	P-value
Grey partridge	Morning	0.108	0.274
	Evening	0.445	0.019
Red-legged partridge	Morning	0.116	0.165
	Evening	0.306	0.008

661 *Different periods of the day (morning, evening) were analyzed separately.*

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664 **Table A6** Six orders of arrangement of broadcast calls according to the sequence prepared.

Sequence number	1 st species	2 nd species	3 rd species
1	Grey partridge	Red-legged partridge	Common quail
2	Grey partridge	Common quail	Red-legged partridge
3	Common quail	Grey partridge	Red-legged partridge
4	Common quail	Red-legged partridge	Grey partridge
5	Red-legged partridge	Common quail	Grey partridge
6	Red-legged partridge	Grey partridge	Common quail

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Table A7 Origin of calls used to prepare audio sequences for the grey partridge, the red-legged partridge and the common quail.

Species	Call position	Author	Source	File name	Date	Time	Country
Grey partridge	1 st and 2 nd calls	Jean C. Roché	<i>Oiseaux d'Europe et du Maghreb (CD)</i> ¹	Perdrix grise.mp3	-	-	-
	3 rd call	Krzysztof Deoniziak	xeno-canto ²	XC247485	01/06/2015	21:00	Poland
	4 th call	Peter Boesman	xeno-canto ²	XC280950	28/05/2008	06:50	Belgium
	5 th call	David M.	xeno-canto ²	XC288385-T05	08/01/2012	07:19	UK
Red-legged partridge	1 st call	Jean C. Roché	<i>Oiseaux d'Europe et du Maghreb (CD)</i> ¹	Perdrix rouge.mp3	-	-	-
	2 nd call	David M.	xeno-canto ²	XC284092	25/04/2013	21:03	UK
	3 rd call	David M.	xeno-canto ²	XC197092-T02	03/07/2013	20:53	UK
Common quail	1 st call	Jean C. Roché	<i>Oiseaux d'Europe et du Maghreb (CD)</i> ¹	Caille des blés.mp3	-	-	-
	2 nd call	Cedric Mrozko	xeno-canto ²	XC256801	03/07/2015	15:00	Portugal
	3 rd call	Piotr Szczypinski	xeno-canto ²	XC252505	12/06/2015	07:30	Poland
	4 th call	Peter Boesman	xeno-canto ²	XC280955	26/05/2007	11:15	Belgium
	5 th call	Tomas Belka	xeno-canto ²	XC80610	27/05/2015	14:00	Portugal
	6 th call	vprannila	soundcloud ³	Viiriäinen	25/05/2015	-	Finland

671
672 ¹ Roché, J.C. (2001). *On Oiseaux d'Europe et du Maghreb* [CD]. Sittelle-Ceba.
673 ² Xeno-canto Foundation, & Naturalis Biodiversity Center. (2005). Xeno-canto Partager les sons
674 d'oiseaux du monde entier. Retrieved February, 2016, from <http://www.xenocanto.org/>
675 ³ SoundCloud Limited. (2016). SoundCloud. Retrieved February, 2016, from <https://soundcloud.com/>
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680 **Table A8** Estimation of the expected number of point counts hosting grey and red-legged partridges

Richness estimator	Grey partridge	Red-legged partridge
Chao 2	98.313	156.375
Jackknife 1	81.250	135.000
Jackknife 2	97.083	158.667
Bootstrap	65.031	110.211
<i>Mean of estimations</i>	<i>85.419</i>	<i>140.063</i>

681 according to the richness estimator.

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686 **Table A9** Sampling error calculated as the percentage of false negative point counts (i.e. the
687 proportion of points considered as free of partridges while the species is present but not detected).

	Grey partridge	Red-legged partridge
Total number of sampled points	490	490
Observed number of points with a species occurrence	53	90
Estimated number of points with species occurrence	85	140
Proportion of false negative points	7.3%	12.5%

688

689 **Figure legends**

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691 **Figure 1** (a) Location of the two study sites in the Maine-et-Loire (1b) and Deux-Sèvres (1c)
692 departments, central western France. (b) Distribution of the point count stations in Maine-et-Loire.
693 (c) Distribution of the point count stations on the LTSER "Zone Atelier Plaine & Val de Sèvre". White
694 dots refer to points sampled from 2016 to 2017, black dots refer to points sampled in 2017 only.
695

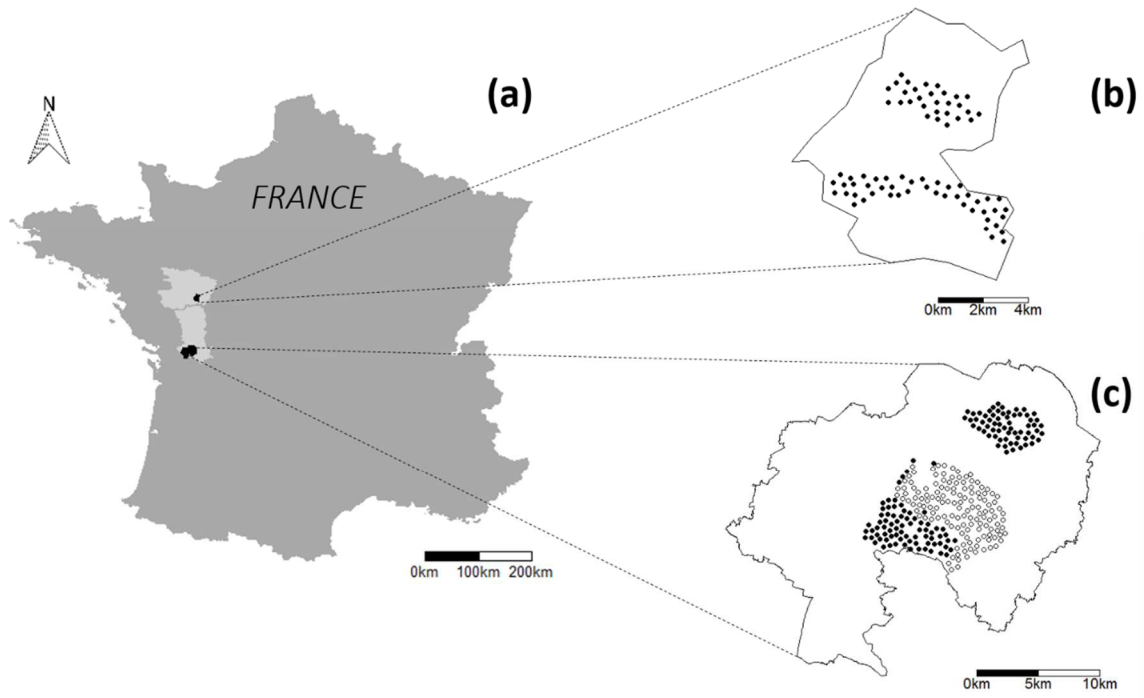
696 **Figure 2** Rates of territorial response for grey (a) and red-legged (b) partridges according to the
697 broadcast stimuli (conspecific, heterospecific, or control calls), assessed from a playback stimuli
698 experiment carried out in two interspecific situations (Alone: point count where only the focus
699 species was observed; co-occurrence: both partridge species were observed; see Methods for more
700 details).
701

702 **Figure 3** Comparison of territorial behaviours of grey (top) and red-legged (bottom) partridges, alone
703 (light-grey) or in co-occurrence areas (dark-grey). Four behavioural metrics were considered:
704 *territorial response rate, calling behaviour, response latency* and *territoriality score* (see Table A2 in
705 Appendix A for more details). (a) and (c) show the distribution of the Linear Discriminant Function for
706 grey and red-legged partridges, respectively. Horizontal bars represent 95% confidence intervals of
707 bootstrapped "alone" linear discriminant scores. (b) and (d) show the correlations in the first
708 dimension (first axis) of the four variables.
709

710 **Figure 4** Daily distribution of the territorial response rate of grey (top) and red-legged (bottom)
711 partridges according to the morning time deviation from sunrise (left) and evening time deviation
712 from sunset (right), assessed by playback experiment in 2016 and 2017. Solid lines represent the
713 response rate of each species where alone, dashed lines the response rate where both species co-
714 occurred.
715

716 **Figure 5** Habitat niche of grey (a) and red-legged (c) partridges when alone and in co-occurrence with
717 the other species (b, d respectively). The solid and dashed lines illustrate respectively 100% and 50%
718 of the available environment. A white arrow indicates a significant shift from the niche centroid in
719 absence to the niche centroid in presence of the second species. (e) represents the correlation circle
720 of the PCA describing the environmental space available in the study area. PC1 and PC2 show the
721 inertia of the first two axes of the PCA.
722

723 **Figure A1** Cumulated number of point counts with occurrence of (a) grey, and (b) red-legged
724 partridges, as a function of the number of the sampling session. Dashed lines correspond to 95%
725 confidence intervals.

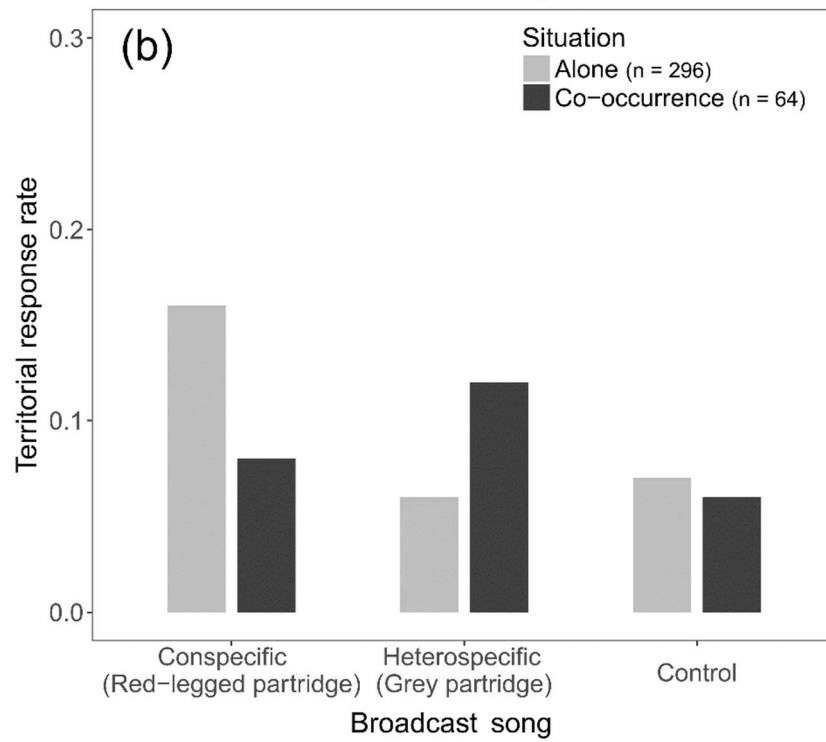
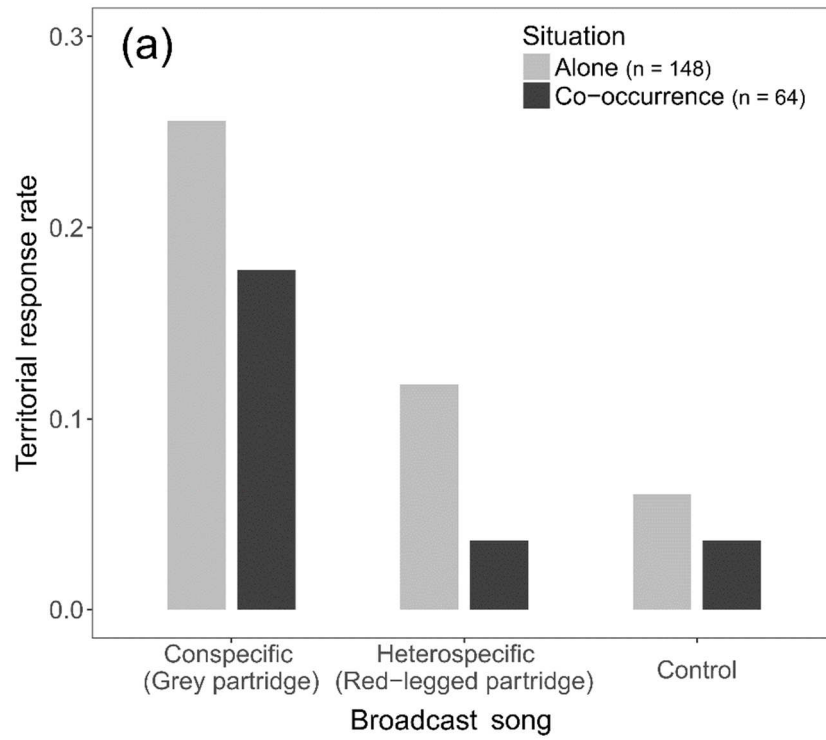


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727 **Figure 1**

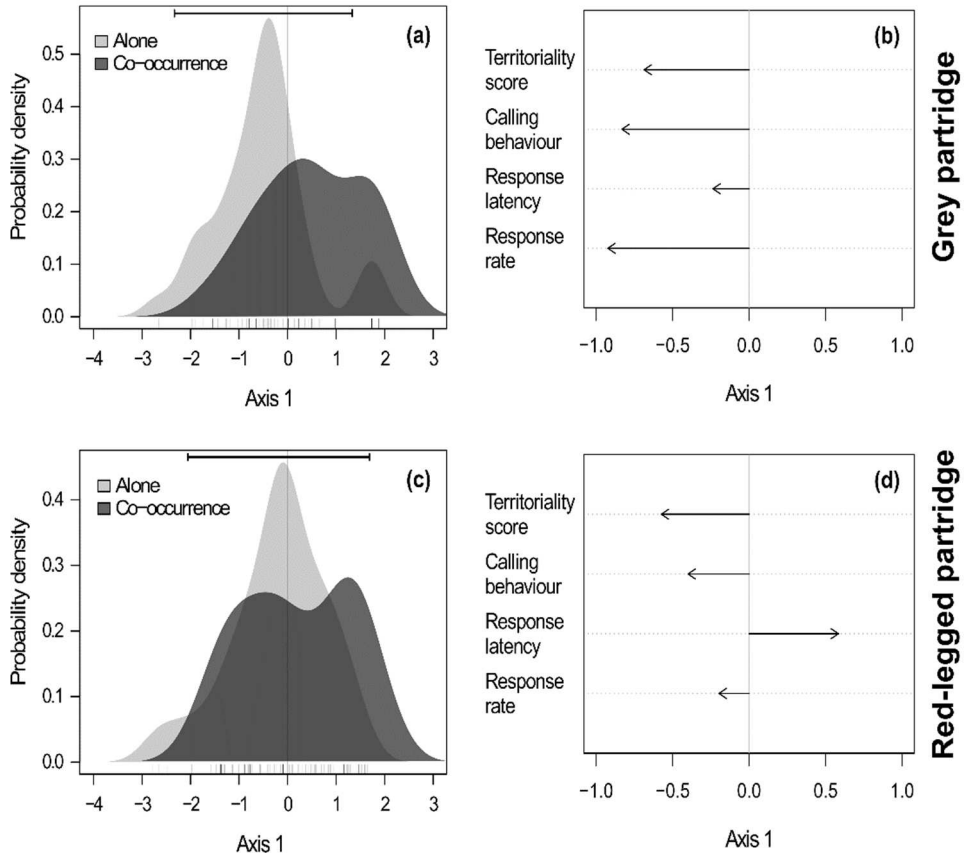
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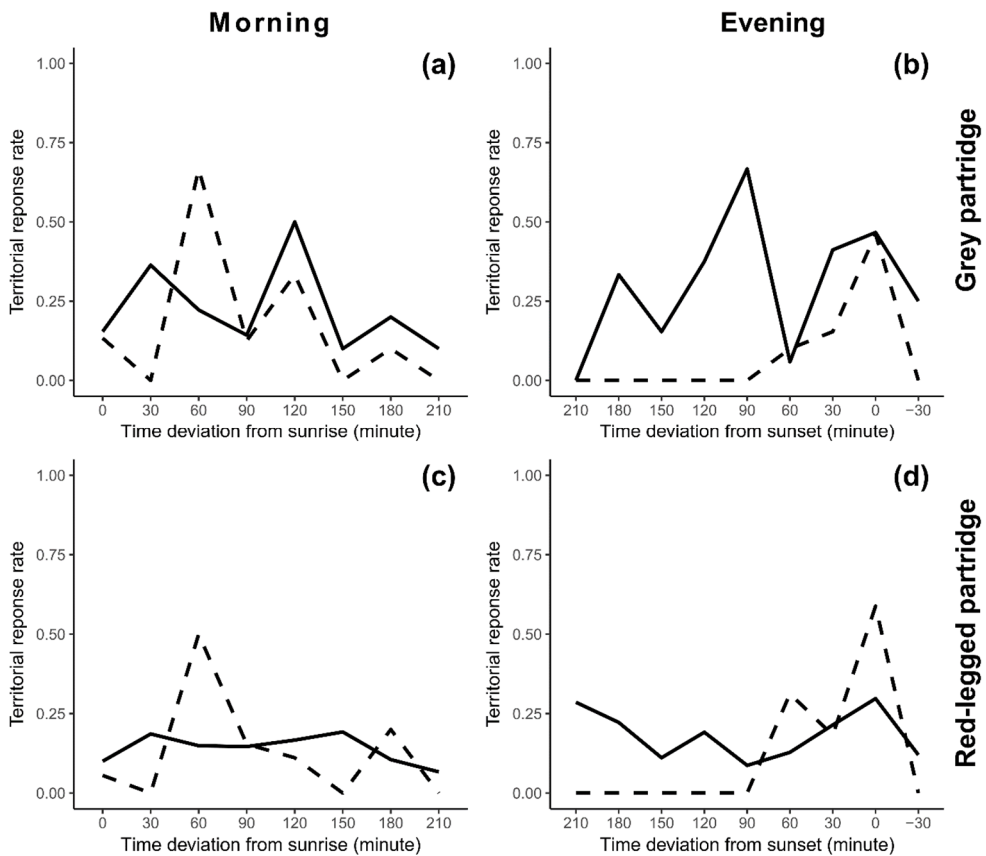
Figure 2



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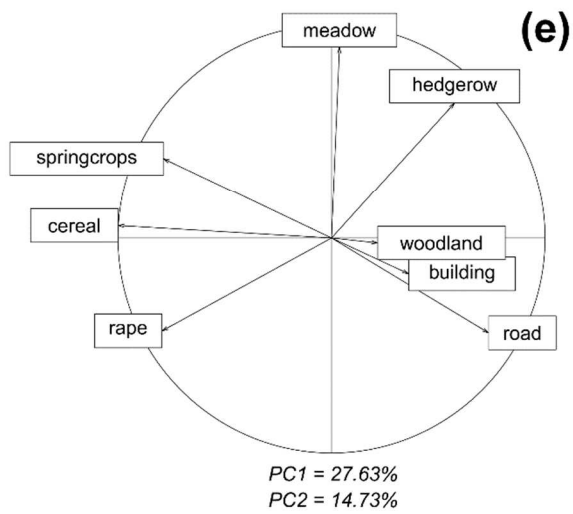
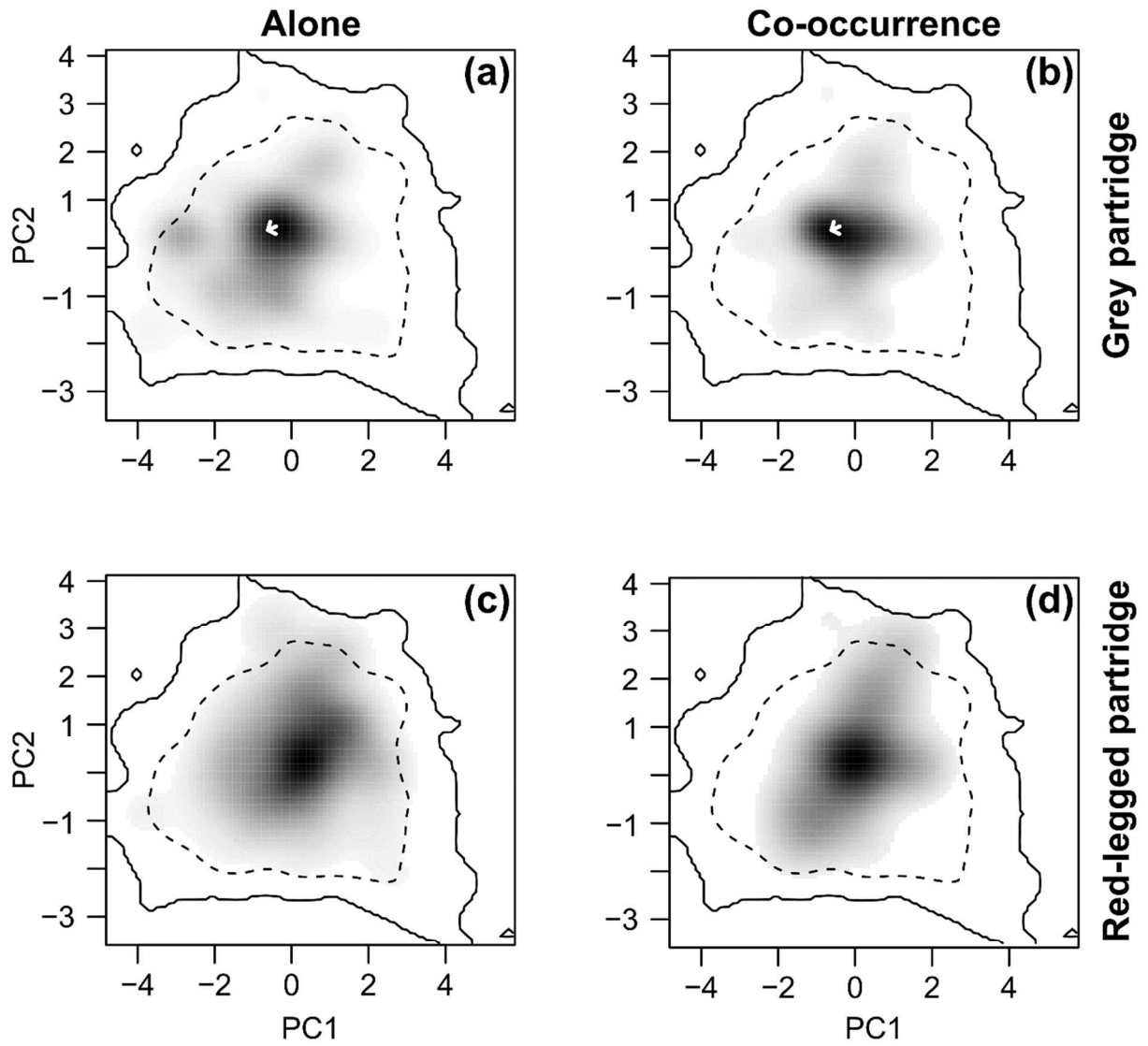
735 **Figure 3**

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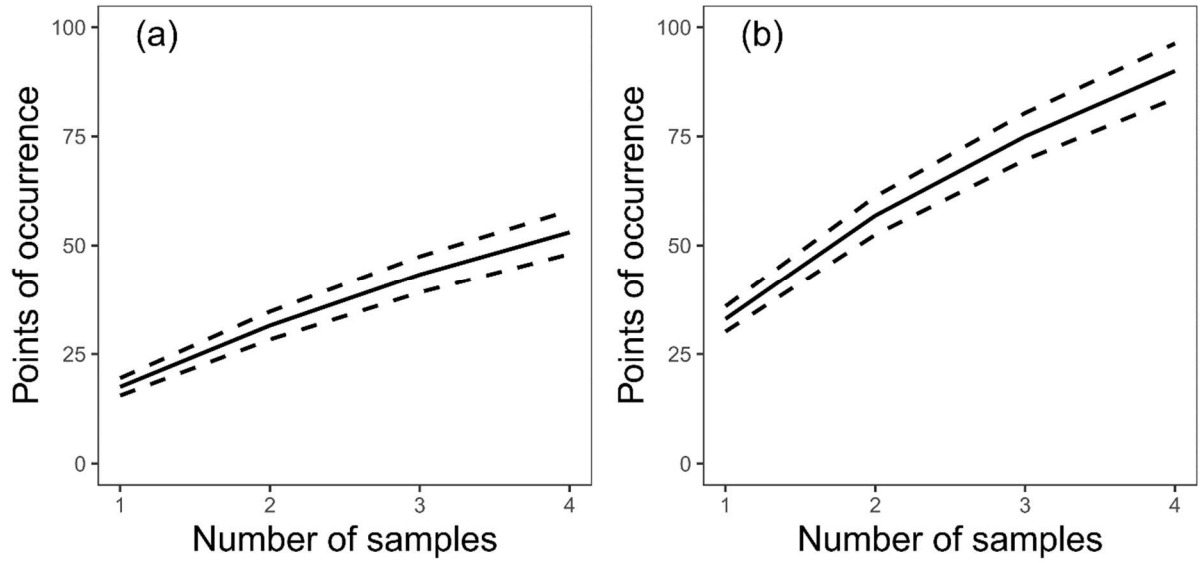
738 **Figure 4**
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741 **Figure 5**

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Figure A1