



Interspecific competition between two partridges in farmland landscapes

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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*, and red-legged, *Alectoris rufa*, 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 analysed territorial behaviour through a playback stimuli experiment and investigated shifts in habitat niche in the 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 shifted its habitat niche away from the latter, 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 they 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.

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Interspecific competition is a major driver of trophic interactions (MacArthur & Levins, 1964), and may define ecological niches (Diamond, 1978; Martin & Martin, 2001b), determine biogeographical patterns (Bull, 1991; Jankowski, Robinson, & Levey, 2010) and affect evolutionary processes (Svårdson, 1949; Wiens, 1992). It is expected to occur between phylogenetically close species sharing limiting resources (Wiens, 1992), either indirectly through resource depletion (Dhondt, 2012; Schoener, 1983) or directly through agonistic interactions (Persson, 1985; Wiens, 1992). The latter are in most cases asymmetric in vertebrates (Martin, Freshwater, & Ghalambor, 2017; Pasch, Bolker, & Phelps,

2013; Persson, 1985; Schoener, 1983): in an analysis of phylogenetically close bird species, 224 of 270 species pairs showed asymmetric agonistic interactions, benefiting the larger species in 87% of cases (Martin et al., 2017). Typically, larger and dominant species show little difference in territorial response (vocal behaviour and approaches) to heterospecific and conspecific songs, while smaller (subordinate) species respond less to the heterospecific song (Martin & Martin, 2001a; McEntee, 2014). This may result in a shift in the song schedule to avoid territorial interaction (Brumm, 2006; Cody & Brown, 1969) and in the displacement and/or contraction of the ecological niche of the subordinate species (Jankowski et al., 2010; Martin & Martin, 2001b; Svårdson, 1949; Tarjuelo, Traba, Morales, & Morris, 2017). These asymmetric outcomes may impact population dynamics of the subordinate species, by constraining its distribution to lower-quality habitats, resulting

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in lower breeding success and/or survival (Martin et al., 2017; Martin & Martin, 2001b).

Recent declines in rural landscape habitat quality, the result of postwar changes in agricultural practices, has not only triggered a decline in European farmland birds (Benton, Vickery, & Wilson, 2003; Newton, 2004; Robinson & Sutherland, 2002), but also aggregated surviving bird populations into the remaining local patches of suitable habitat (Aebischer & Ewald, 2012). While an increasing likelihood of interspecific competition should be expected in these habitats (Newton, 2004; Robillard, Garant, & Bélisle, 2013), the implications for farmland bird declines or population recovery limitation has remained largely unexplored (but see Robillard et al., 2013). The grey partridge, *Perdix perdix*, and red-legged partridge, *Alectoris rufa*, are phylogenetically related and belong to the Phasianidae (Wang, Kimball, Braun, Liang, & Zhang, 2013). They were originally parapatric, showing separate but contiguous distributions (Cramp & Simmons, 1980; see also; Watson, 1962; Bull, 1991), with the grey originating from central Europe and Asia (Liukkonen-Anttila et al., 2002) and the red-legged from Iberia (Ferrero et al., 2011). Originally, the distributional contact zone was primarily restricted to central and southern France and northwest Italy (Cramp & Simmons, 1980). However, huge releases of red-legged partridges as gamebirds in the U.K. and France (Aebischer, 2019; Cramp & Simmons, 1980) resulted in the current situation where both species are sympatric over vast areas of western Europe. Both species select open agricultural landscapes (Aebischer & Kavanagh, 1997; Aebischer & Lucio, 1997; Potts, 1980) and have similar breeding habitats (Bro et al., 2013; Green, Rands, & Moreby, 1987; Rands, 1988), although slight differences in micro-habitat exist (Meriggi, Montagna, & Zacchetti, 1991). They also overlap in their breeding phenology (egg laying in May–June, peak of territorial activity in February–April; Rotella & Ratti, 1988). In addition, chicks feed on the same arthropod taxa, while adults shift to leaves and seeds (Bro & Ponce-Boutin, 2004; Green, 1984; Green et al., 1987). Finally, partridges are highly territorial, with both mates contributing to territory defence (Casas, Arroyo, Viñuela, Guzmán, & Mougeot, 2016; Potts, 1980). The original narrow contact zone between both species was suggestive of the presence of competition interactions (Bull, 1991; Watson, 1962). These can now be expected to be present over the entire, vast, contact zone (Jankowski et al., 2010; Martin & Martin, 2001a; McEntee, 2014).

The possible increased competition pressure from the introduction of the larger and bulkier red-legged partridge in the human-created contact zone (Carpio et al., 2017; Robertson, 1996; Sokos, Birtsas, & Tsachalidis, 2008) has rarely been studied as a possible cause of grey partridge decline or as a limiting factor in population recovery (Bro, 2016; Meriggi et al., 1991). However, while the grey partridge is one of the most iconic farmland birds in Europe (Sotherton, Aebischer, & Ewald, 2014), it has declined strongly over the last few decades (Aebischer & Kavanagh, 1997; Aebischer & Potts, 1994) and is now threatened at national or subnational scales (Charra & Sarasa, 2018; Eaton et al., 2015). In this study, we investigated behaviours that might potentially indicate interspecific competition between the two partridges, in study areas located within the original area of sympatry (central western France). We quantified territorial behaviour through playback stimuli, analysing the patterns of territorial response in single- and two-species situations (Cody & Brown, 1969; Martin & Martin, 2001a), and further investigated behavioural (territorial daily activity) and habitat niche shifts in the area of co-occurrence. Based on the asymmetric interspecific competition hypothesis, we predicted that grey partridge (smaller species) should respond less to the call of the red-legged partridge than to the conspecific call in both the absence and the presence of red-legged partridge, and should show lower levels of agonistic behaviour in areas of co-occurrence. Conversely, red-

legged partridge should increase its territorial response to grey partridge in co-occurrence situations, while maintaining or increasing its agonistic behaviour. We also predicted that grey partridge should restrict their daily activity pattern when co-occurring with red-legged partridge to minimize interspecific encounters. Finally, habitat niche of the putatively subordinate grey partridge should shift when in co-occurrence with red-legged partridges, while the putatively dominant red-legged partridge should be unaffected by the presence of grey partridge.

METHODS

Study Area

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

Survey Protocol and Playback Tests

We first established a grid of playback stations with a cell size of 500 m (excluding built-up areas) to locate territorial pairs accurately (the size of a single home range is about 20 ha in spring/summer: Birkan, Serre, Skibnienski, & Pelard, 1992). Sample points were placed as close as possible to the centroid of the grid cells, but still on a path or a road for ease of access and to minimize disturbance. Each sample point was surveyed four times per year, with two sessions in the morning and two in the evening, as patterns of daily vocal activity peak at dawn and dusk (Pépin & Fouquet, 1992). Sample points were slowly approached by car; the observer then went out quietly and waited for 1 min before starting a session. A session consisted of broadcasting, at fixed volume (calibrated to be heard up to 250 m away to avoid overlap between neighbouring points) with a NEWONLINE N74 speaker, an audio sequence containing territorial calls of males of both study species (155 s for each species) and of the common quail, *Coturnix coturnix*, as a control. For each species, bouts were separated by 1 min periods of silence (see Appendix 2 for more details about sequence preparation and call origins). Since calls of three species were broadcast, six audio sequences containing the six possible combinations of broadcasts were prepared and one of them was randomly played at each session. In 2016, surveys were conducted at 140 playback stations at ZAPVS (6–25 April), while in 2017, 275 stations were surveyed at ZAPVS and 75 at METL, from 14 March to 28 April. Surveys involved tracks of 14–17 sampling points along a road/path, with each track corresponding to a sequence of points made in the morning or evening session. Tracks were made alternately in one way then in the other, to avoid hourly biases in the sequence of points.

For each point in a year, we determined whether none, one or the two species were present, if contacted at least once over the four sampling sessions. Points were then classified into four distinct categories as to whether none, only one or both partridges were

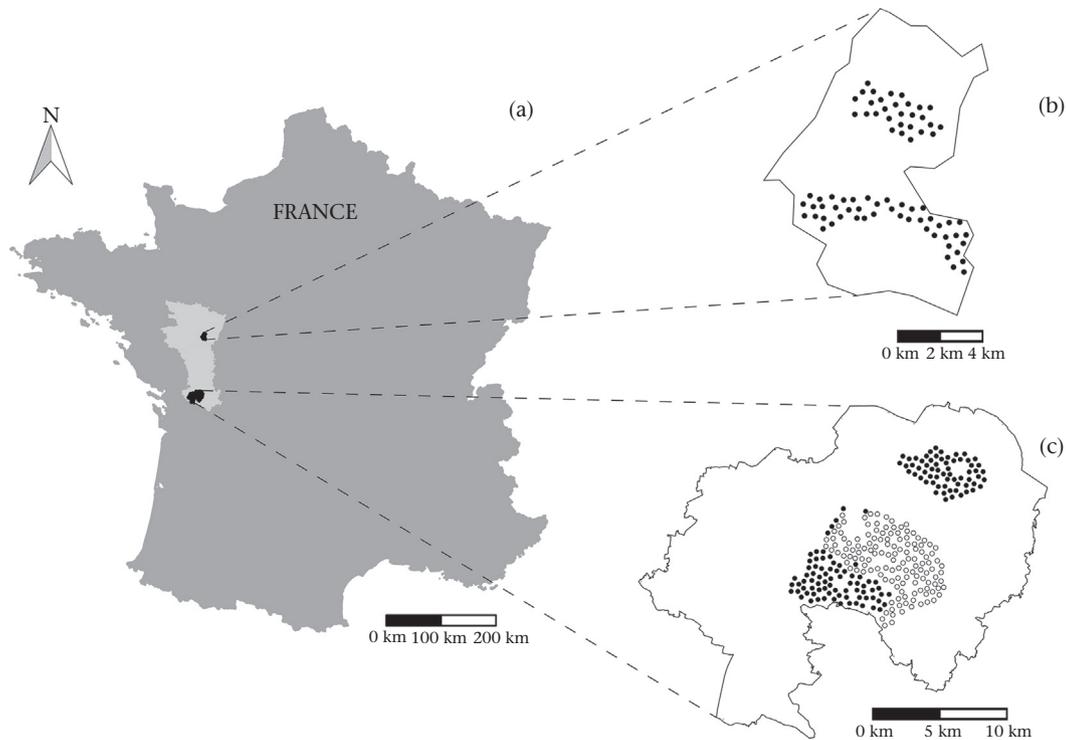


Figure 1. (a) Location of the two study sites in the Maine-et-Loire and Deux-Sèvres departments, central western France. (b) Distribution of the point count stations in Maine-et-Loire. (c) Distribution of the point count stations on the LTSER 'Zone Atelier Plaine & Val de Sèvre'. White dots refer to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

contacted. The 'no contact' category was discarded, so that only points with at least one occurrence were kept for analyses, assuming that a species was absent at a point if no sighting was recorded there across the four sampling sessions. We checked whether discarded points might contain partridges by using rarefaction curve analyses (see [Appendix 3](#)): only 7.3% and 12.5% of points for grey and red-legged partridges, respectively, may have been removed erroneously. For each individual contacted at a point, we noted the playback call that elicited the response, the type of response (0: no response; 1: response to one of the partridge species calls; 2: response to both partridge stimuli), the latency of response (elapsed time between the beginning of the playback and any territorial response) and territorial behaviour (walking approach, flight approach, calling).

Ecological Habitat Description

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

From the annually collected land cover data, we then created a grid of 600 x 600 m² cells, using R ([R Core Team, 2017](#)) and QGIS ([Quantum GIS Development Team, 2017](#)), excluding all pixels that had less than half their area (18 ha) lying within the study site. Pixel size was chosen as the minimal size that contained sufficient numbers of pixels with (1) only grey partridge occurrences over 2013–2017 ($N = 115$), (2) only red-legged partridge occurrences ($N = 137$) or (3) both partridge species ($N = 32$). Analysed landscape metrics were based on those identified as being selected (either positively or negatively) by grey and/or red-legged partridges ([Birkan et al., 1992](#); [Bro et al., 2013](#); [Harmange et al., 2019](#); [Meriggi et al., 1991](#); [Rands, 1987](#)): cereals, rape, meadows, spring crops (corn, sunflower etc.), hedgerows, roads/tracks, woodlands and buildings. Landscape metrics used in analyses corresponded to the surface area (or total length in m) of each habitat had in the pixel, divided by the pixel surface area (to account for any edge effect). Each parameter was calculated annually from 2013 to 2017, except for roads and hedgerows, which remained stable and for which we set only one layer ([Harmange et al., 2019](#)).

Ethical Note

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

Statistical Analyses

Territorial behaviour

We used generalized linear mixed models (binomial response variable, logit link) to investigate presence/absence of each species' territorial response (vocalization and/or approach) using the lme4 R package (Bates, Maechler, Bolker, Walker, & Christensen, 2018), as a function of the interaction between playback stimuli (broadcast species) and the interspecific situation (target species alone or in co-occurrence with the other species). The playback sequence (six levels) and the rank of partridge call (first or second position) were considered as random factors. When needed, Tukey's multiple comparison tests were performed using the R package emmeans (Lenth, Singmann, Love, Buerkner, & Herve, 2019). For each species, we further analysed the magnitude of territorial response, described by four parameters calculated for each point count station: territorial response rate (number of responding individuals within pairs, 0/1/2); response latency (s); calling behaviour (0: no response; 1: response to one of the two partridge species' calls; 2: response to both partridge stimuli); and a territoriality score in the form of a ranking of increasing territorial behaviour intensity (0: no response; 1: approach; 2: vocalization; 3: approach with vocalization; 4: flying approach with vocalization; see Appendix 1 Table A2 for more details on calculations). Then, for each species, we carried out linear discriminant analyses (James & McCulloch, 1990) to investigate whether territorial behaviour (described from the four behavioural variables) allowed discrimination between the two interspecific situations, i.e. when a single species was observed and when both species co-occurred. Linear discriminant analyses allowed the difference between two situations (alone or co-occurrence) to be maximized statistically for each species using a discriminant function assessed from four observed territorial behaviours. This analysis was performed using the MASS R package (Ripley, 2017). To handle the differences in sample sizes between the two situations (alone or co-occurrence) given the low sample size of the 'co-occurrence' category, we produced 95% confidence intervals (CI) for linear discriminant scores following Luttrell and Lohr (2018). The CI were assessed by generating bootstrap samples with replacement and simulating 1000 sets for the 'alone' category (highest sample size) with reduced sample size equal to the smaller 'co-occurrence' set. The mean of the linear discriminant scores \pm SD for each of the 1000 bootstrapped samples was calculated and a 95% CI was computed for the 'alone' category. Finally, we carried out analyses of variance (ANOVA) to test whether each territorial behaviour (see above) contributed significantly to discriminating the two interspecific situations (species alone versus co-occurrence).

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

Habitat niche modelling

Within-species habitat niches were analysed with data from 2013–2017, averaging environmental layers across years for each

pixel. Three types of occurrences (2013–2017) were considered: (1) grey partridge only (at least once) in the pixel over the 5 years ($N = 222$); (2) red-legged partridge only ($N = 192$); (3) grey ($N = 64$) and red-legged ($N = 52$) partridges co-occurring, each being recorded at least once (but not necessarily simultaneously). To compare species' niches in the presence of a single species versus in co-occurrence of the two species, we used Broennimann et al. (2012)'s niche modelling framework implemented in the ecospat R package (Broennimann, Di Cola, & Guisan, 2016). The first step consists of describing the environmental space available in the study area, using the first two axes of a principal component analysis (PCA-env) performed on all pixels, with each environmental layer being a different variable in the PCA. Then, for each species in each situation (species alone or in co-occurrence), a smoothed density of occurrences in the PCA-env space is obtained using a kernel density function. This allows niche space to be graphically delineated, for each situation, as a relative abundance index ranging from 0 (environmental conditions in which the species was not observed) to 1 (environmental conditions in which the species was most commonly observed), thus handling between-group differences in the number of occurrences. Niche overlap can then be calculated (e.g. between grey alone and grey co-occurring with red-legged partridge), using Schoener's D index (Warren, Glor, Turelli, & Funk, 2008) which ranges from 0 (no overlap) to 1 (full overlap). The niche equivalency test, a commonly used niche randomization test, was performed (Broennimann et al., 2012; Warren et al., 2008). In this test, the two occurrence data sets are mixed, and two new data sets are reconstituted randomly (1000 times), conserving the sizes of the two original data sets. The distribution of the 1000 D niche overlap values from the paired simulated data sets are then compared with the observed value of D : if the latter is outside the 95% range for the simulated values, the null hypothesis is rejected, i.e. the observed niches are less equivalent than expected by chance (Broennimann et al., 2012; Warren et al., 2008). All statistical analyses were performed using R software (R Core Team, 2017).

RESULTS

Territorial Behaviour

Among the surveyed points (combining both study sites), there were 21 and 106 points (2016 and 2017, respectively) with at least one species in one of the four sampling sessions. Assuming that the presence of an individual in at least one sampling session for a given point count reflected the presence of a territorial pair, 37 points (7.5%) with grey partridge, 74 (15.1%) with red-legged partridge and 16 (3.3%) with both species were recorded. We found that grey partridge territorial responses were significantly influenced both by the broadcast species and whether red-legged partridge co-occurred (Table 1): they responded more to the conspecific than to the heterospecific or control call (Fig. 2a, Appendix 1 Table A3), but co-occurrence with red-legged partridge significantly reduced the grey partridge response (Fig. 2a, Appendix 1 Table A3). Similarly, territorial responses of red-legged partridge, when alone, were higher to the conspecific call than the grey partridge or control call (Fig. 2b, Table 1, Appendix 1 Table A3). Unlike the grey partridge, the red-legged demonstrated a balanced response whichever the species when co-occurring with grey partridge (Fig. 2b, Appendix 1 Table A3).

Scores of territorial behaviour in response to playback (from the four behavioural variables) allowed discrimination between situations when grey partridges were alone or co-occurring with red-legged partridges. The results suggested a shift in the territorial

Table 1

Results of generalized linear mixed models (binomial response variable, logit link) considering the territorial response (vocal behaviour and/or approaches) of grey and red-legged partridges as response variable

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

Explanatory variables are the broadcast species (control, grey partridge, red-legged partridge) and the interspecific situation (alone, co-occurrence). Modalities in italics are considered as references. All models include the playback sequence ($N = 6$) and the rank ($N = 2$) of the partridge broadcast calls (grey partridge or red-legged partridge broadcast first) as a random effect.

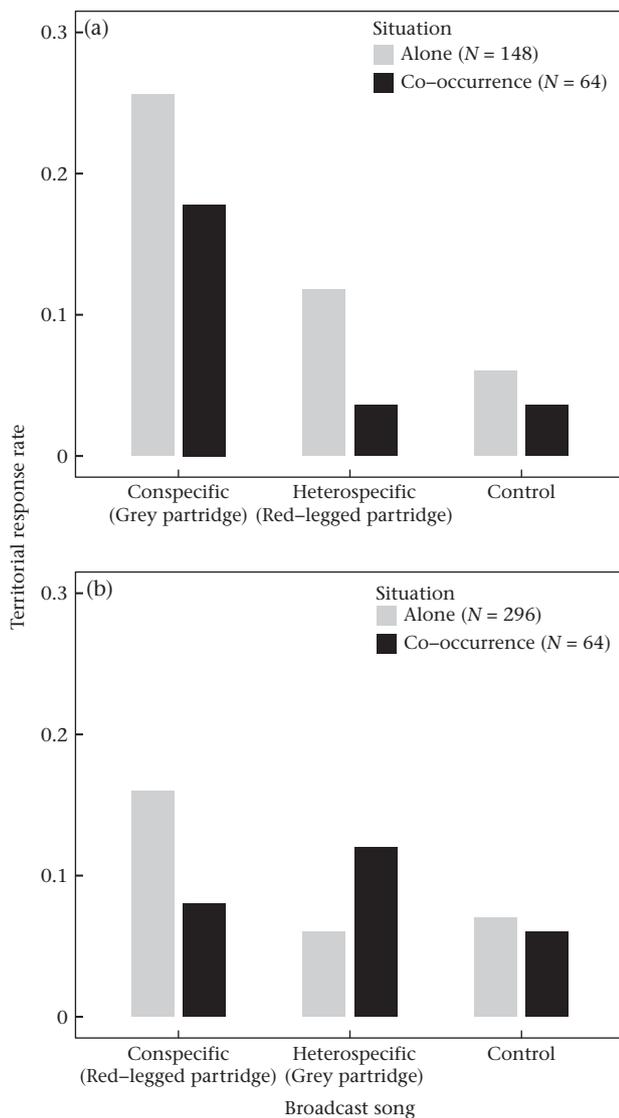


Figure 2. Rates of territorial response for (a) grey and (b) red-legged partridges according to the broadcast stimuli (conspecific, heterospecific or control calls), assessed from a playback stimuli experiment carried out in two interspecific situations (alone: point count where only the focus species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

behaviour of the grey partridge in co-occurrence situations (Fig. 3a). Territorial response rate, calling behaviour and territoriality score were the three highest contributing variables discriminating territorial behaviour between the two situations (Fig. 3b) and in situations of co-occurrence the grey partridge reduced its response rate, number of calls and intensity of territorial response (i.e. territorial score) significantly (ANOVA, Appendix 1 Table A4). In contrast, no significant differences appeared for any of the four behavioural variables in the red-legged partridge responses (ANOVA, Appendix 1 Table A4), indicating no shift in behaviour like that found for the grey partridge (Fig. 3c) and behavioural variables were very poor contributors in discriminating situations where red-legged were alone or co-occurring with grey partridges (Fig. 3d).

The daily pattern of grey partridge territorial behaviour was significantly affected by co-occurrence with red-legged partridge (Fig. 4, Appendix 1 Table A5): under co-occurrence, grey partridge territorial response became concentrated around the sunset in the evening, while no changes were detected in the morning (Fig. 4). A similar pattern was detected for the red-legged partridge where alone versus in co-occurrence with the grey partridge (Fig. 4, Appendix 1 Table A5).

Habitat Niche

Analysis showed that the grey partridge's habitat niche when alone or when co-occurring with the red-legged partridge overlapped by only 53% (Fig. 5a and b). The equivalency test was significant ($P = 0.02$), indicating that the grey partridge's habitat niche shifted significantly in the presence of the red-legged partridge. In contrast, the red-legged partridge's habitat niche when alone or when co-occurring with the grey partridge showed more overlap (67%; Fig. 5c and d). When co-occurring with the grey partridge, the red-legged's habitat niche did not shift, so remaining equivalent in both situations (equivalency test: $P = 0.55$).

Although Fig. 5a and b suggests a moderate shift, the core of the grey partridge's habitat niche changed in the opposite direction to that of the red-legged partridge, towards greater proportions of spring crop, cereal and rape habitats and lower proportions of meadows and hedgerows (Fig. 5e). Overall, the red-legged partridge's habitat niche was wider, comprising its preferred open arable land (e.g. spring crops, cereals and rape) associated with seminatural permanent cover (meadows and hedgerows), but the species also avoided closed habitats (woodlands and built-up areas; Fig. 5e).

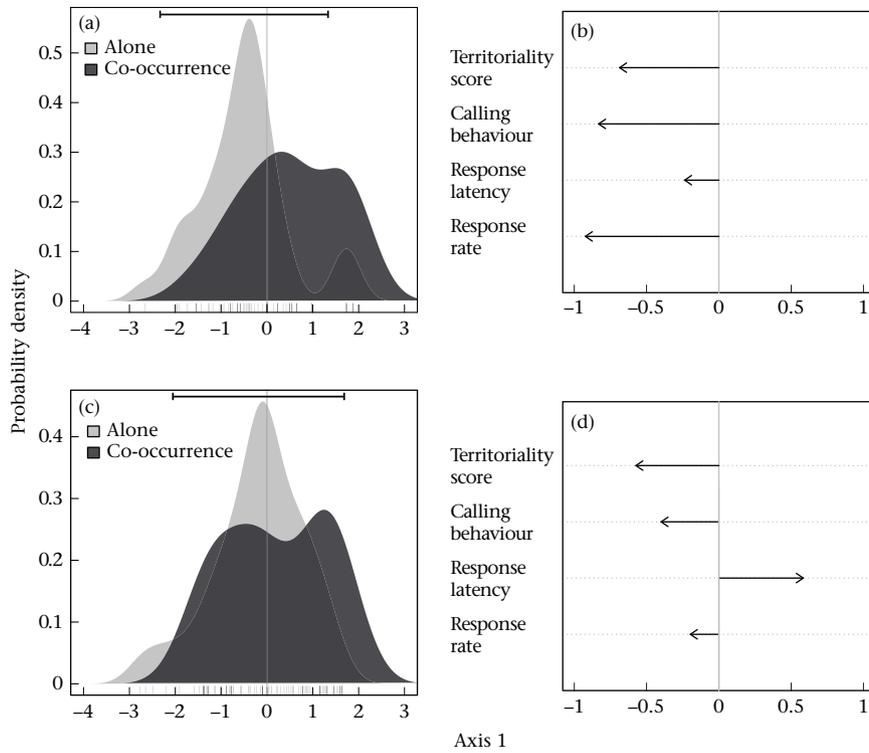


Figure 3. Comparison of territorial behaviours of (a, b) grey and (c, d) red-legged partridges, alone or in co-occurrence areas. Four behavioural metrics were considered: territoriality score, calling behaviour, response latency and territorial response rate (see Appendix 1 Table A2 for more details). (a, c) Distribution of the linear discriminant function for (a) grey and (c) red-legged partridges. Horizontal bars represent 95% confidence intervals of bootstrapped 'alone' linear discriminant scores. (b, d) Correlations in the first dimension (first axis) of the four variables for (b) grey and (d) red-legged partridges.

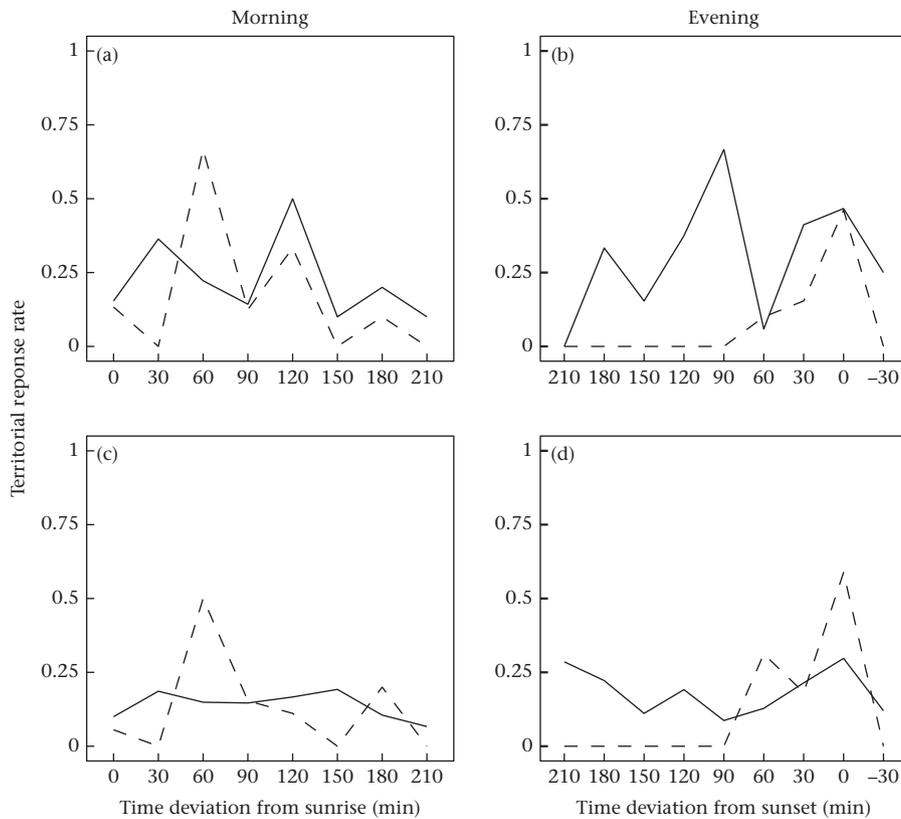


Figure 4. Daily distribution of the territorial response rate of (a, b) grey and (c, d) red-legged partridges according to (a, c) the morning time deviation from sunrise and (b, d) the evening time deviation from sunset, assessed by playback experiments in 2016 and 2017. Solid lines represent the response rate of each species where alone and dashed lines where both species co-occurred.

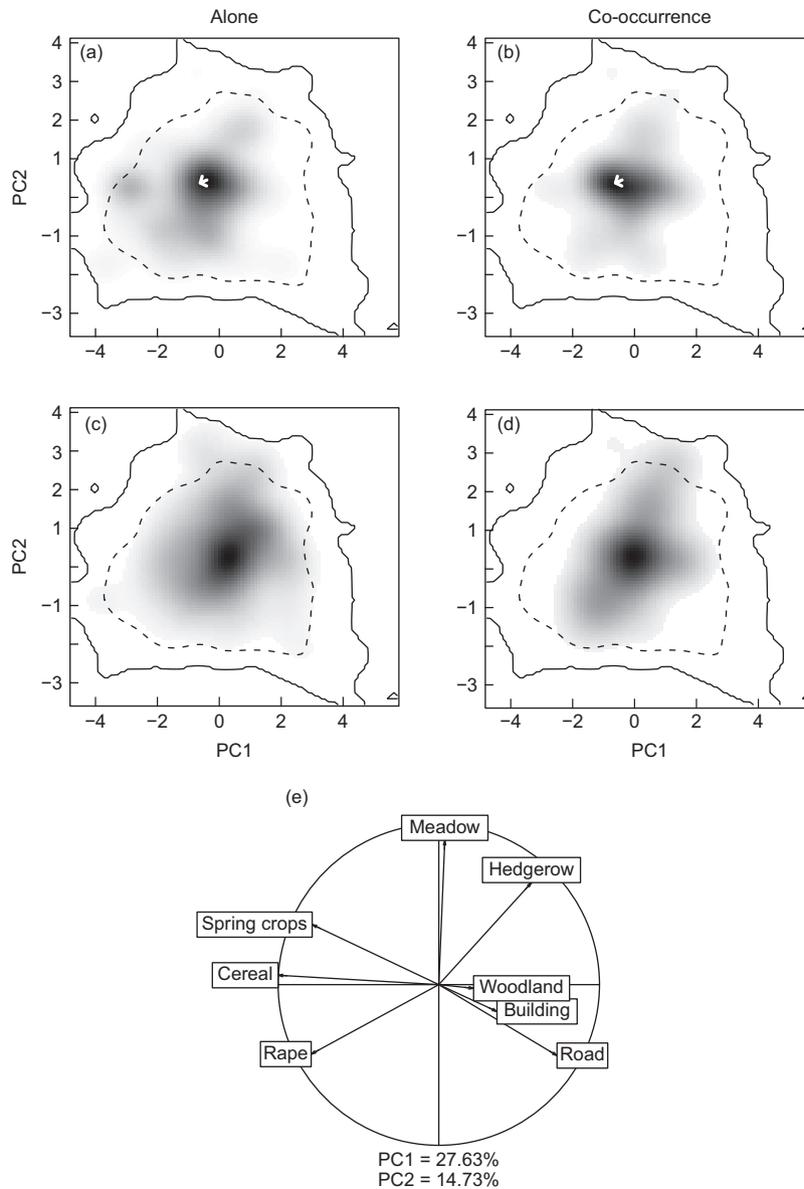


Figure 5. Habitat niche of (a, b) grey and (c, d) red-legged partridges when (a, c) alone and (b, d) in co-occurrence with the other species. The solid and dashed lines illustrate 100% and 50% of the available environment, respectively. A white arrow indicates a significant shift from the niche centroid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

DISCUSSION

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

Such shifts in territorial behaviour intensity towards a more discreet behaviour when facing a competitive species have been documented previously in birds (e.g. [Martin & Martin, 2001a](#); [McEntee, 2014](#)) and other vertebrates, such as mammals (e.g. [Pasch et al., 2013](#)). Indeed, in such cases, the typical response of the subordinate species is to avoid unfriendly interactions with a dominant and larger competitor. Conversely, the red-legged partridge showed a much higher territorial response rate to its own species when alone, but shifted to balanced response rates to both species in situations of co-occurrence. This convergence of

territorial behaviour has already been documented for dominant species involved in asymmetric interspecific interactions ([Jankowski et al., 2010](#); [Pasch et al., 2013](#)) and we can thus reject [Murray's \(1971\)](#) hypothesis, which suggests that interspecific territoriality results from misdirected intraspecific interactions due to incorrect signal recognition. However, huge releases of captive-reared partridges for game management could alternatively explain responses to the heterospecific call, as both partridge species are often reared on the same farms and may have been sensitized or conditioned by early exposure to the heterospecific call. We suggest, however, that this alternative hypothesis is unlikely because both species would then be expected to respond to heterospecific calls (not just to the red-legged partridge) and each species would also be expected to respond to the heterospecific stimuli, whether in the absence of competitors or in co-occurring situations. In addition, we found that both species adjusted their daily territorial activity under co-occurrence, although territorial

activity of both species remained synchronized, while a temporal segregation was expected. This may be the result of too coarse a temporal resolution in our analyses, making temporal shifts in territorial response hard to detect. For instance, Brumm (2006) showed that temporal segregation in territorial activity occurs at a finer scale in nightingales, *Luscinia megarhynchos*, which adjust and focus their vocal activity within the silent intervals between two heterospecific broadcast songs (see also Cody & Brown, 1969). An alternative explanation could be that acoustic differences between partridge calls might have enabled vocal activity to remain synchronized, while ensuring little interspecific interference (Dhondt, 2012; Doutrelant & Lambrechts, 2001).

Finally, we detected a slight habitat niche shift in the less competitive species in situations of co-occurrence with the dominant one, while there was no such shift for the dominant species. This pattern is typical of asymmetric competition for habitat probably resulting from the agonistic behaviour of the dominant species (Jankowski et al., 2010; Martin & Martin, 2001a, 2001b). While the grey partridge (subordinate species) preferentially selects grass along hedgerows to nest (Potts & Aebischer, 1991), its habitat niche shifted to more open habitats (more annual crops and less hedgerows) when co-occurring with the red-legged. These habitats are more subject to human disturbance and may therefore be of poorer quality for breeding (Burel et al., 1998), perhaps causing lower fitness and/or survival (see Martin et al., 2017; Martin & Martin, 2001a, 2001b). This habitat niche shift, probably resulting from interspecific competition, could have also driven the microhabitat segregation observed by Meriggi et al. (1991), with the grey partridge being generally more associated with crops and open lands, while the red-legged is more linked to seminatural elements such as hedgerows.

Asymmetric competition occurring in the contact zone of parapatric species is well known to reduce fitness of the subordinate species (Jankowski et al., 2010; Martin & Martin, 2001a). Such behavioural outcomes of competition may have strong implications for the conservation and management of partridges. Although releasing non-native species has long been used as a strategy to limit hunting pressure on wild native populations (Aebischer & Ewald, 2004; Bro, 2016; Carpio et al., 2017), the huge releases of red-legged partridges in the core area of the grey partridge raise concerns not only for the grey partridge decline, but also for its possible future recovery. The presence of morphologically similar species has long been identified as interfering with the success of re-establishment in translocations (Griffith, Scott, Carpenter, & Reed, 1989). The grey partridge is currently a focus of interest for many reinforcement projects that are identified as the only tool for restoring self-sustaining populations in many areas (Buner & Aebischer, 2008; Buner, Browne, & Aebischer, 2011). However, this has proved inefficient or even counterproductive (Reitz, 2003; Sokos et al., 2008), because of many unintentional but adverse effects on population dynamics (inadvertent shots: in Aebischer & Ewald, 2004; parasite-mediated competition: in Tompkins, Greenman, et al., 2000; Tompkins, Draycott, et al., 2000). Our results suggest further impacts on territorial behaviour and access to resources for the native species, although the effects on demography remain unexplored. Our study thus suggests that the presence of red-legged partridges may limit the chances of success in such projects. Therefore, to quantify the strength of competitive interaction effects on population dynamics, further field experiments are required before formally concluding that interspecific competition occurs between these species. These should include (1) controlling for the origin of birds (natural or captive birds reared on monospecific farms preventing any early contact between species), (2) treatments (deliberately releasing grey partridge only, red-legged only or both species together, in different sites offering the same availability in

environmental conditions) and (3) assessing the influence of species' co-occurrence on demographic parameters (adult survival, nest predation, chick survival; see Martin & Martin, 2001b).

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Appendix 1: Additional Information and Results

Table A1

Grey and red-legged partridge density estimations (mean \pm SD) in the Long-Term Socio-Ecological Research site 'Zone Atelier Plaine & Val de Sèvre' (LTSER ZAPVS) and the Maine-et-Loire 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) |

Estimations were derived from playback experiments of 2016 and 2017.

Table A2

Description of behavioural variables considered in the analysis of territorial behaviour, and predictions under a hypothetical asymmetric competition for the dominant and subordinate species

| 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 between the beginning of the broadcast call and the vocal response) recorded over the four sampling sessions | In co-occurrence areas, 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 conspecific and heterospecific partridge calls responded to by individuals. 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 which is expected to respond to both conspecific and heterospecific calls and low for a subordinate species which is not expected to respond 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 have a higher territoriality score when co-occurring with the subordinate one, while the reverse was expected for the subordinate species (see Jankowski et al., 2010 ; Martin & Martin, 2001a) |

Metrics were calculated for each species, from each point count.

Table A3

Tukey's multicomparison post hoc tests computed after generalized linear mixed models (binomial response variable, logit link) performed on the territorial response of grey and red-legged partridge species

| Species | Variable | Estimate | SE | z | P |
|----------------------|---|----------|-------|--------|--------|
| 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 |

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

Table A4

Effect of the independent variable interspecific situation (Alone, Co-occurrence) on the territorial behaviour of grey and red-legged partridges

| Species | Dependent variables | Independent variables | <i>t</i> | <i>df</i> | <i>P</i> | 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 | |

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

Table A5

Cramer–von Mises' distribution tests comparing the territorial response rates of grey and red-legged partridges in single-species versus co-occurring situations

| Species | Period | <i>t</i> | <i>P</i> |
|----------------------|---------|----------|----------|
| 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 |

Different periods of the day (morning, evening) were analysed separately.

Appendix 2. Broadcast Calls and Playback Sequences

Each audio sequence contained three phases, corresponding to the territorial call of the grey partridge, the red-legged partridge and the common quail (Table A6). For each species, the audio phases were prepared to last around 155 s by repeating calls from at least three different individuals (Table A7), to avoid territorial calls being intimidating (Novoa, 1992). In each audio sequence, species phases were separated by 1 min of silence. Audio sequences were broadcast randomly, while making sure that the grey partridge's call was displayed as the first call of the sequence at least once (morning or evening) for each survey point.

Table A6

Six orders of arrangement of broadcast calls according to the sequence prepared

| Sequence number | First species | Second species | Third 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 |

Table A7

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

| Species | Call position | Author | Source | File name | Date | Time | Country |
|----------------------|------------------------|--------------------|--|--|-------------------|------|----------|
| Grey partridge | First and Second calls | Jean C. Roché | Oiseaux d'Europe et du Maghreb (CD) ¹ | Perdrix grise.mp3 | – | – | – |
| | Third call | Krzysztof Deonizak | Xeno-canto ² | XC247485 | 1 Jun 2015 | 2100 | Poland |
| | Fourth call | Peter Boesman | Xeno-canto ² | XC280950 | 28 May 2008 | 0650 | Belgium |
| | Fifth call | David M. | Xeno-canto ² | XC288385-T05 | 8 Jan 2012 | 0719 | U.K |
| | Red-legged partridge | First call | Jean C. Roché | Oiseaux d'Europe et du Maghreb (CD) ¹ | Perdrix rouge.mp3 | – | – |
| Red-legged partridge | Second call | David M. | Xeno-canto ² | XC284092 | 25 Apr 2013 | 2103 | U.K |
| | Third call | David M. | Xeno-canto ² | XC197092-T02 | 3 Jul 2013 | 2053 | U.K |
| Common quail | First call | Jean C. Roché | Oiseaux d'Europe et du Maghreb (CD) ¹ | Caille des blés.mp3 | – | – | – |
| | Second call | Cedric Mrozko | Xeno-canto ² | XC256801 | 3 Jul 2015 | 1500 | Portugal |
| | Third call | Piotr Szczypinski | Xeno-canto ² | XC252505 | 12 Jun 2015 | 0730 | Poland |
| | Fourth call | Peter Boesman | Xeno-canto ² | XC280955 | 26 May 2007 | 1115 | Belgium |
| | Fifth call | Tomas Belka | Xeno-canto ² | XC80610 | 27 May 2015 | 1400 | Portugal |
| | Sixth call | vprannila | SoundCloud ³ | Viiriäinen | 25 May 2015 | – | Finland |

¹ Roché, J.C. (2001). *Oiseaux d'Europe et du Maghreb* [CD]. Sittelle-Ceba.

² Xeno-canto Foundation & Naturalis Biodiversity Center. (2005). Xeno-canto Partager les sons d'oiseaux du monde entier. Retrieved February 2016 from <http://www.xenocanto.org/>.

³ SoundCloud Limited. (2016). SoundCloud. Retrieved February 2016 from <https://soundcloud.com/>.

Appendix 3. Estimation of Sampling Error

We assessed the sampling error as the proportion of point counts considered without any partridge, whereas a species is present but not detected. To do this, we performed a rarefaction analysis using PAST (Hammer, Harper, & Ryan, 2001).

For each species, we first drew the cumulative curves of point

counts where the species was detected as a function of sampling session rank (Fig. A1). The rarefaction curves revealed that our sampling was not exactly exhaustive as a plateau was not reached.

Then, we estimated the total number of point counts expected to host each species (Table A8). As several estimators can be used to

do this, we ran four estimators and then averaged them to obtain a synthetic index. This analysis revealed that on average 85 point counts may host grey partridges and 140 may host red-legged partridges (Table A8). Finally, we calculated the proportion of false negative point counts (i.e. the species is present but not detected) according to the following function (Table A9):

$$\frac{\text{Number of false negative points}}{\text{Number of observed negative points}} \times 100$$

$$= \frac{\text{Estimated number of occurrence points} - \text{Observed number of occurrence points}}{\text{Total number of sampled points} - \text{Observed number of occurrence points}} \times 100$$

counts where the species was detected as a function of sampling session rank (Fig. A1). The rarefaction curves revealed that our sampling was not exactly exhaustive as a plateau was not reached.

Then, we estimated the total number of point counts expected to host each species (Table A8). As several estimators can be used to

Therefore, we can consider that the sampling error is about 7.3% for the grey partridge and 12.5% for the red-legged partridge (Table A9).

Table A8

Estimation of the expected number of point counts hosting grey and red-legged partridges according to the richness estimator

| 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 |
| Mean of estimations | 85.419 | 140.063 |

Table A9

Sampling error calculated as the percentage of false negative point counts (i.e. the 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 a species occurrence | 85 | 140 |
| Percentage of false negative points | 7.3 | 12.5 |

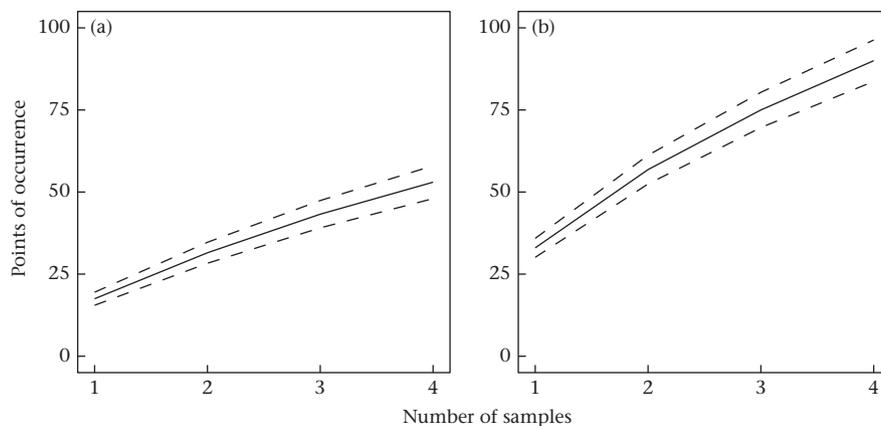


Figure A1. Cumulated number of point counts with occurrence of (a) grey and (b) red-legged partridges, as a function of the number of the sampling session. Dashed lines correspond to 95% confidence intervals.