



# Are population changes of endangered little bustards associated with releases of red-legged partridges for hunting? A large-scale study from central Spain

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## Abstract

The release of farm-reared game birds for hunting is an increasingly common game management practice. However, releasing could have negative effects on sympatric wild species, for example, through parasite transmission. Here, we document the spatial-temporal patterns and intensity of red-legged partridge releases in the province of Ciudad Real, Spain, over a 15-year period (2002–2016), relating them to local changes in the abundance of little bustards estimated from two surveys carried out in 2005 and 2016. Within the province, > 600,000 red-legged partridges were released annually over at least 20% of the area. Releasing intensity varied between estates and fluctuated over the 15-year study period, probably because of an economic crisis during 2008–2014. Overall, numbers of little bustards dropped by 46% between surveys, the decrease being more marked in the west of the province. Contrary to expectation, the only hunting estates where little bustards did not decrease were those with higher release intensity. This may be a consequence of management measures or other factors that benefit little bustards and are more prevalent on those estates than elsewhere, such as game crop provision, predator control or habitat quality.

**Keywords** *Alectoris rufa* · Farm-reared birds · Game crops · Management · Population decrease · *Tetrax tetrax*

## Introduction

Hunting and its management have changed markedly throughout human history (Washburn and Lancaster 2017)

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and are currently undergoing a process of intensification in parts of Europe. For example, practices like the release of farm-reared game birds with the aim of increasing hunting stock have become increasingly common (Arroyo and Beja 2002; Aebischer 2019). In the case of small-game species, this sometimes involves the release of millions of birds (Mondain-Monval and Girard 2000; Noer et al. 2008; Champagnon et al. 2009; Caro et al. 2014; VKM 2017; Aebischer 2019). However, this practice carries many potential problems for the wild populations of released species (Champagnon et al. 2012): changes in behaviour, demography and morphology, dissemination of pathogens or genetic introgression in wild populations (Tompkins et al. 2000; Villanúa et al. 2006; Arroyo and Beja 2002; Champagnon et al. 2010; Champagnon et al. 2012; Díaz-Fernández et al. 2013). Furthermore, it may also affect sympatric species owing to competition for resources or spread of pathogens (Prenter et al. 2004; Bicknell et al. 2010), although positive effects associated with habitat management have also been reported (Mustin et al. 2018).

The red-legged partridge (*Alectoris rufa*; hereafter RLP) is one of the game species released for hunting in Europe

(Arroyo and Beja, 2002), with millions being released annually in the UK, France and Spain (Tupigny 1996; Caro et al. 2014; Aebischer 2019). The RLP is numerically and socially a very important quarry species in Spain (Andueza et al. 2018), being hunted in 94% of the small-game estates of central Spain (Ríos-Saldaña 2010). Official data report annual hunting bags of between 2.5 and 4 million RLPs in that country (MAAMA 2014), a figure that could exceed the wild RLP breeding population, estimated at 1.7–3.7 million pairs (Blanco-Aguilar et al. 2004). This is only possible through the release of farm-reared RLPs for hunting, which has intensified in Spain in recent decades with several millions of RLPs released annually (Caro et al. 2014).

Releasing as a management practice is controversial (Sokos et al. 2008; Gamborg and Jensen 2017; Mustin et al. 2018; Avery 2019), even within the hunting sector (Delibes-Mateos et al. 2014; Delibes-Mateos et al. 2015; Gamborg et al. 2016). In Spain, the main perceived benefit of releases is economic, as it is seen as the only way to maintain commercial hunting (Delibes-Mateos et al. 2015). However, releases (as currently carried out) do not necessarily help the recovery of wild populations, which they can for instance contaminate genetically (Blanco-Aguilar et al. 2008; Casas et al. 2012). Farm-reared RLPs also host a greater quantity and range of pathogens than do wild partridges (Millán et al. 2004; Pagès-Manté et al. 2007), and releases of farmed RLPs can expose wild birds to disease (Millán et al. 2004; Villanúa et al. 2008; Díaz-Sánchez et al. 2012a, b). Importantly, RLP releases have the potential to affect not only wild partridges but also other sympatric species. For example, the little bustard (*Tetrax tetrax*) is a protected steppe bird characteristic of Spanish cereal farmland areas, whose populations have decreased by 48% in Spain during the last decade (2005–2016; García de la Morena et al. 2018). Villanúa et al. (2007) described the occurrence of a new parasite for this species that apparently originated from released RLPs, which could potentially cause a problem. On the other hand, little bustards are more abundant on hunting estates with high levels of fox control than elsewhere (Estrada et al. 2015), and predator control is more intensive on estates that release high numbers of RLPs (Arroyo et al. 2012).

This study had two main objectives: first, to document the spatio-temporal dynamics of RLP releases in the Ciudad Real province (central Spain) and second, to assess whether these releases are associated with changes in the local population of the little bustard in this province. As Ciudad Real is one of the Spanish provinces where partridge releasing is numerically important (Ríos-Saldaña 2010) and is also a stronghold for little bustard in the Iberian Peninsula (García de la Morena et al. 2018; Casas et al. 2019), we compared population changes of little

bustards between hunting estates characterised by different levels of releasing intensity.

## Methods

### Study area

Data were collected in the province of Ciudad Real (19,813 km<sup>2</sup>), located on the Spanish southern plateau. It holds one of the highest densities of breeding little bustards in Spain (García de la Morena et al. 2018). It is also one of the most important areas in Spain for hunting RLPs (Blanco-Aguilar et al. 2003). More than 80% of the area of Ciudad Real consists of privately managed hunting estates. In most cases, the owner of the hunting rights is not the same as the owner of the land (Arroyo et al. 2012). A range of management measures are frequently implemented with the aim of improving RLP hunting, the commonest being the provision of supplementary food (grain) and water, predator control and releases of farm-reared partridges (Arroyo et al. 2012).

### Red-legged partridge releases

A hunting estate wanting to release farm-reared RLPs in Spain needs to have this specified explicitly in its Hunting Technical Plan (a document reassessed by the administration every 5 years, specifying the hunting intentions for the following years) and must also make an official request to the provincial game office just before the release. We obtained and analysed data from these official requests in Ciudad Real from 2002 to 2016. Our data refer to minimum numbers of released birds, as there may have been hunting estates releasing partridges without complying with the regulation (i.e. without making an official request beforehand). However, we consider that, even if not complete, our data provide a reliable source for estimating spatial and temporal trends of releases, as there is not, in principle, any bias in the type or location of estates providing information.

Technically, the release of farm-reared RLPs is carried out mainly as part of “population reinforcement” and can legally occur only outside the hunting season. However, most releases take place in late summer, usually as close as possible to the opening of the hunting season (Caro et al. 2014). In addition, some hunting estates are legally labelled “intensive” or “commercial”. In these intensive hunting estates, there are no legal restrictions on the number or timing of farm-reared RLP releases, so releases take place throughout the hunting season and usually in very large numbers (Arroyo et al. 2012). In Ciudad Real, around 6% of hunting estates are “intensive” (official data of JCLM).

For each hunting estate requesting a permit to release RLPs to the provincial game office between 2002 and 2016, we

collected data on the number of birds released, its area, perimeter, location and whether it was legally labelled as “intensive” or “commercial”. With this information, we mapped the distribution of hunting estates that had released partridges between 2002 and 2016 using QGIS (QGIS Development Team 2018).

### Temporal patterns of red-legged partridge releases

We graphically compared trends in the total number of RLPs released each year on intensive and non-intensive hunting estates separately, in the number of hunting estates that released partridges each year by type of hunting estate and in the annual number of birds released per hectare by type of hunting estate.

### Little bustard abundance

Two national little bustard surveys were carried out in Spain during the breeding seasons (April and May) of 2005 and 2016 (García de la Morena et al. 2006; García de la Morena et al. 2018). We used information from these surveys for the province of Ciudad Real. The surveys were carried out in UTM cells of  $10 \times 10$  km ( $100 \text{ km}^2$ ) that comprised potentially suitable habitat for little bustard. Each  $100\text{-km}^2$  cell was subdivided into four  $25\text{-km}^2$  squares, sampling only the  $25\text{-km}^2$  square at the southwest of the  $100\text{-km}^2$  square. Within each chosen  $25\text{-km}^2$  square, 20 points were sampled by noting all little bustards heard or seen within a 250-m radius. In 2016, the same sampling design was used in an attempt to resample the same exact points. In total, 48  $25\text{-km}^2$  squares were sampled in both years. Other squares were sampled in only one of the years (either 2005 or 2016). We restricted analyses to sampling points monitored in both surveys (695 points), which represented 69.2% of all points sampled in 2005. We calculated the density of little bustard males within each circle with radius of 250 m (19.61 ha). We considered only males because females were much less detectable (García de la Morena et al. 2006).

### Analysis of change in little bustard density

We examined the change in numbers of little bustards by fitting a generalised linear mixed model (GLMM) with Poisson error and logarithmic link, within a Bayesian framework (*stan\_glmer* function of *rstanarm* package in R; Gabry and Goodrich 2018). Our response variable was the number of male little bustards observed at each point. As explanatory variables, we included year, date (as a categorical variable with six levels, i.e. six periods from early April to late May) and hour (as a categorical variable with 10 levels, 10 periods from sunrise to sunset); we included sampling point identity as a random factor. Hour was included to account for changes in

detectability throughout the day (greatest in early morning and late afternoon, lowest at mid-day; García de la Morena et al. 2006), and date was included to allow for changes in detectability as bustard behaviour and habitats changed as the season progressed (García de la Morena et al. 2006). We built the model in a Bayesian framework to address convergence issues using a standard GLMM approach (*lme4* package in R; Bates et al. 2015). The *stan\_glmer* function performs Bayesian estimation via a Markov chain Monte Carlo process. According to the default settings, this function fits four Markov chains with 2000 iterations each and 1000 interactions per chain are burned as a warm-up process. We evaluated the convergence of Markov chains using Gelman Rubin R-hat statistics (values  $< 1.1$ ). We used the *estimate* package in R (Makowski et al. 2019) to obtain, through our model, the mean abundance of little bustard per year, its 95% credible intervals and the percentage population change.

To map the spatial variation in little bustard population change between 2005 and 2016, we used the 48  $25\text{-km}^2$  squares sampled in both surveys. Each  $25\text{-km}^2$  square was subdivided into squares measuring 100 by 100 m (1 ha), and to each 1-ha square, we attached a smoothed density of little bustard males in a given survey calculated as (number of individuals within 1 km of the centre point of the square)/(area surveyed within 1 km of the square point) as proposed by Watson et al. (2007). For each 1-ha square, we then calculated the natural logarithm of the ratio between male densities in 2016 and 2005 (adding 0.5 to each value to avoid zeros). We plotted those values spatially using QGIS (QGIS Development Team 2018).

We built another model for checking statistically the spatial distribution of population change. We calculated the natural logarithm of the ratio between male numbers counted in 2016 and 2005 (adding 0.5 to each value to avoid zeros) at each sampling point. First, we checked the variogram for spatial correlation among points (Webster and Oliver 2007) and found none. We then built GAM models, using *mgcv* R package (Wood 2003), to assess potential non-linearity in the relationship between population change and longitude or latitude. We found that the relationship with longitude was linear, but that with latitude seemed quadratic. We subsequently built a GLM in R, including as explanatory variables longitude, latitude, latitude squared and the interactions between longitude and the two latitude variables. Longitude and latitude were standardised before analysis using the formula  $(x - \text{mean}(x))/\text{sd}(x)$ .

### Relationship between releases and changes in abundance of little bustard

We used only information on RLP releases carried out in the period between the two national little bustard surveys, from

2005 to 2015 (releases of 2016 were not used because they occurred after the 2016 little bustard survey), and selected all hunting estates that included little bustard survey points in both years (2005 and 2016). Hunting estates were grouped into four categories of release intensity based on the frequency of releases and the number of birds released per ha, which should reflect the probability of restocked birds coming into contact with wild ones (Online resource 1). Categories were as follows: (i) no release: hunting estates where no release had officially been done in any of the study years ( $n = 90$ , average size = 20.20 km<sup>2</sup>); (ii) low-intensity releases: releases occurred in less than 5 of the study years with fewer than 4 partridges per ha ( $n = 14$ , average size = 36.18 km<sup>2</sup>); (iii) medium-intensity releases: releases occurred in more than 5 study years, with 4 to 15 partridges per ha ( $n = 6$ , average size = 23.63 km<sup>2</sup>); (iv) high-intensity releases: releases were made in more than 5 study years with more than 15 partridges per ha ( $n = 6$ , average size = 42.43 km<sup>2</sup>). To these, we added a fifth category for the patches of land that included a survey point and were not hunting estates (non-hunting areas,  $n = 234$ , average size = 0.3 km<sup>2</sup>). The latter were more numerous than hunting estates, but each of them was much smaller in size (as they mainly related to small disjunct areas between hunting estates).

To estimate little bustard abundance in each of those hunting estates (or non-hunting areas) and survey year, we calculated little bustard density at each sampled point as number of males counted per survey area (19.61 ha). Then using QGIS, we determined the total sampled area in each hunting estate (or non-hunting area) as the sum of the areas of the sampled circles that were inside each hunting estate. We estimated the number of male little bustards in the sampled area as [(little bustard density in each circle  $\times$  area of this buffer inside each estate)]. Finally, we divided the number of little bustards by the total sampled area (in km<sup>2</sup>) to estimate the density of little bustards (birds per km<sup>2</sup>) in each hunting estate or non-hunting area.

Using these data, we fitted a GLMM model (*nlme* R package; Pinheiro et al. 2019) to  $\ln(\text{little bustard density} + 1)$ . To examine spatial effects, we included year, standardised longitude, standardised latitude, the square of standardised latitude and the interactions between longitude and the two latitude variables as explanatory variables, and the ID of hunting areas as a random effect. We included the area sampled on each hunting estate as a weight in the models. We then augmented the model by adding hunting estate category and its interactions with the spatial variables as further explanatory variables. We used Tukey HSD post hoc test for comparisons between estate categories (*lsmeans* R package; Russell 2016). All analyses were carried out with R v3.5.1 (R Core Team 2018), and graphics were produced with the package *ggplot2* of R (Wickham 2016).

## Results

### Spatial and temporal patterns of red-legged partridge releases

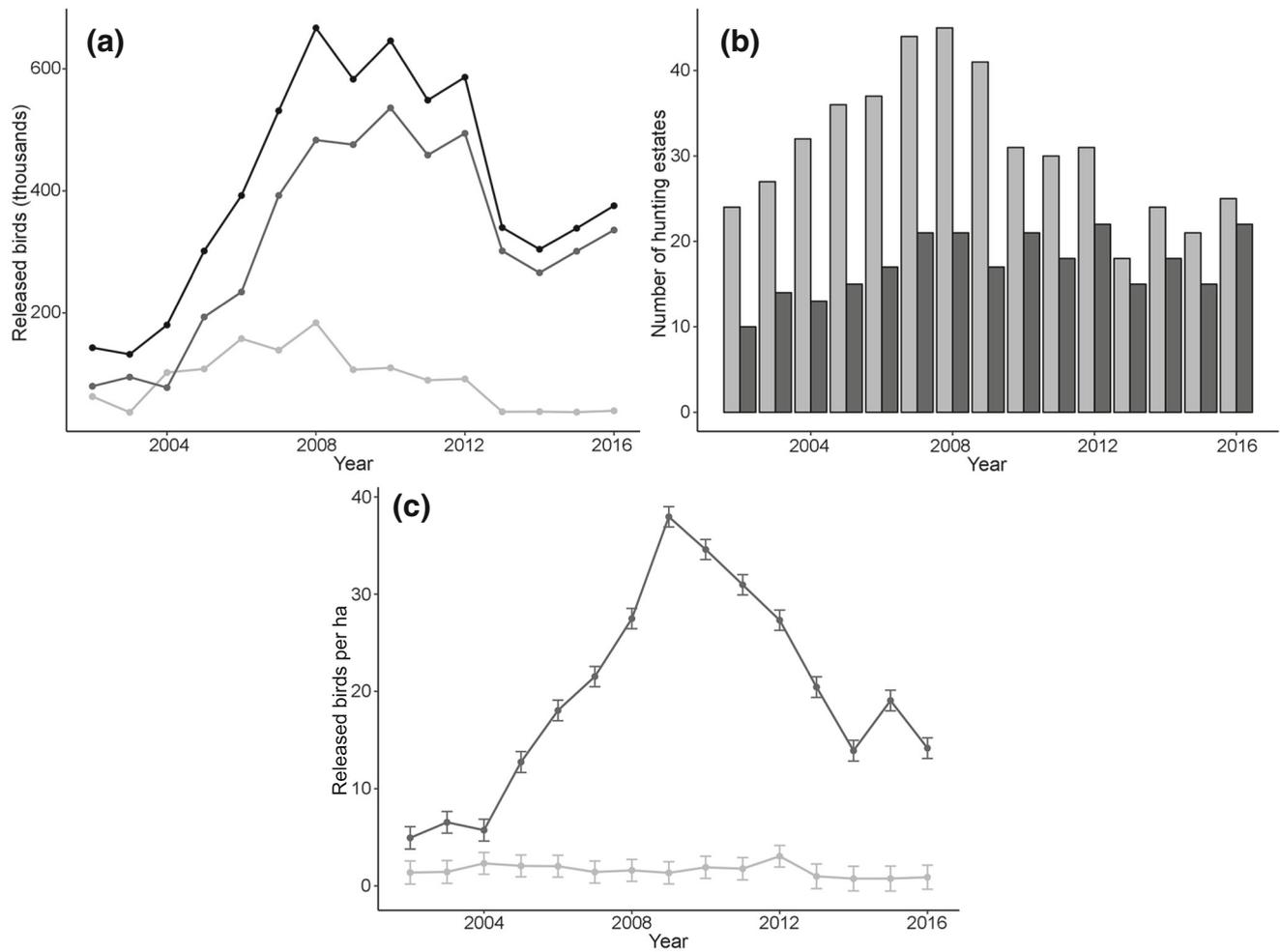
Between 2002 and 2008, the number of hunting estates releasing RLPs doubled, and the overall numbers of RLPs released annually in Ciudad Real increased four-fold (Fig. 1). The increase in overall numbers released was due mainly to the intensive hunting estates, which constituted a third of the hunting estates where releasing took place and where the number of birds released per hectare increased eight-fold (Fig. 1). By contrast, the lower increase in released birds on non-intensive hunting estates was due to a greater number of estates releasing, not to a rise in the number of released birds per ha (Fig. 1).

From 2009 to 2016, the overall number of released RLPs approximately halved, although trends differed according to the type of hunting estate. On the non-intensive hunting estates, this change was again mainly due to a decrease in the number of hunting estates that released, as the number of released RLPs per ha declined only after 2013 (Fig. 1). On the intensive hunting estates, the number of released partridges per ha decreased strongly after 2010, while the number of hunting estates releasing was maintained (Fig. 1). On these intensive estates, the number of released partridges started to increase again from 2014 (Fig. 1). Spatially, releases of RLPs in Ciudad Real were mainly concentrated in the south-eastern part of the province, although large estates with non-intensive releasing were also present in the north and north-east (Fig. 2). Non-intensive hunting estates that released RLPs covered an area of 3343.56 km<sup>2</sup>, while intensive hunting estates covered 545.98 km<sup>2</sup>. This meant that partridge releases occurred in at least 20% of the area of the Ciudad Real province.

### Changes in little bustard abundance

We found that little bustard counts varied according to sampling date and sampling hour (Fig. 3). The number of little bustards counted per point peaked in mid-April, then declined in mid-May, increasing again in late May. Regarding the sampling hour, more birds were counted in the early morning and in the late afternoon than in the middle of the day (Fig. 3). In addition, we observed an overall significant decrease between 2005 and 2016 (non-overlapping 95% Bayesian credible intervals) of little bustard counts from 0.413 (95% CI 0.342–0.493) to 0.224 (95% CI 0.177–0.271) birds per point ( $n = 695$  sampled points) in 2005 and 2016 respectively, representing a difference of  $-45.8\%$  (95% CI 30.7–60.9%).

Little bustard population change was not homogeneous across the province, and decreases appeared more pronounced in the east (Fig. 4). A GLM analysis confirmed this pattern,

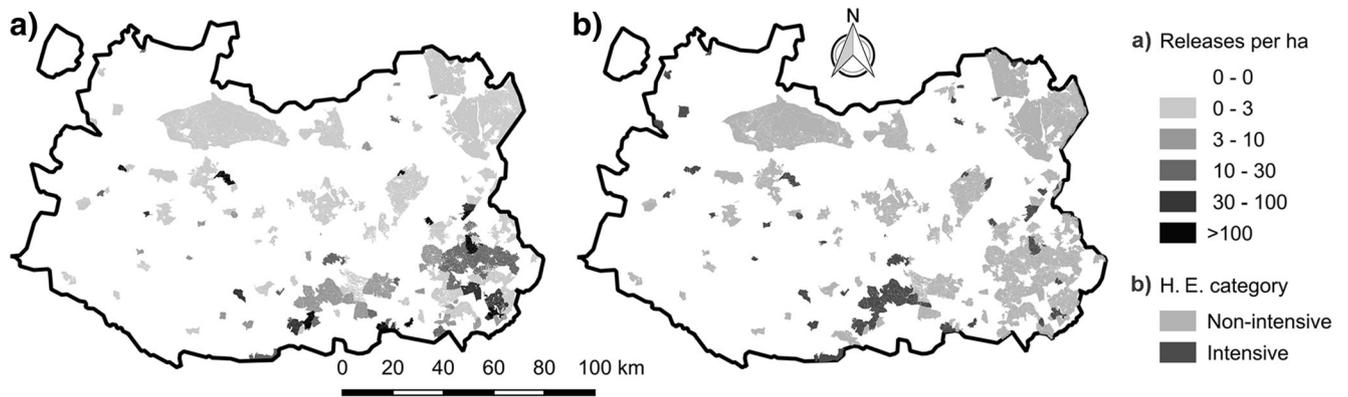


**Fig. 1** Temporal trends in farm-reared RLP releases in Ciudad Real, Spain, during 2002–2016. **a** Total annual number of birds released (in thousands) on all estates (black line), on non-intensive estates (light grey) and on intensive estates (dark grey). **b** Number of non-intensive (light

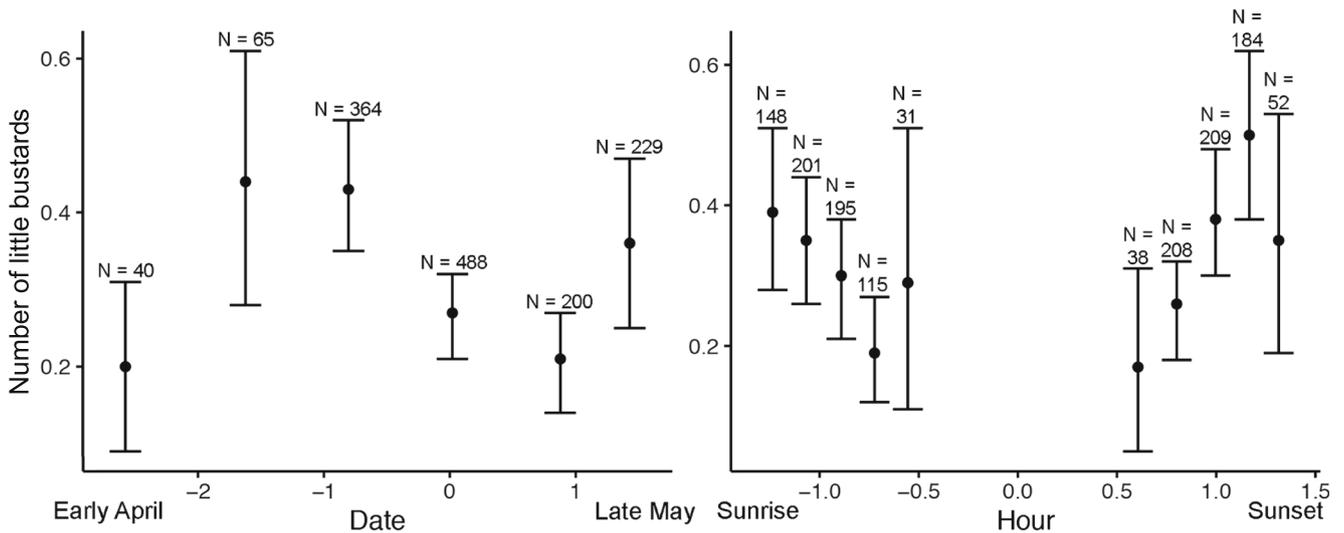
grey) and intensive (dark grey) hunting estates that released partridges each year. **c** Annual mean ( $\pm$  SE) number of partridges released per ha on non-intensive (light grey) and intensive (dark grey) hunting estates

showing a positive linear relationship between population change and longitude (Table 1). The effect of latitude was quadratic, with lower decreases in the north and south of the province (Table 1). The interaction between longitude and

quadratic latitude was significant, the slope of latitude being more pronounced in the south than in the north and the quadratic effect of longitude being more marked in the east than in the west (Table 1).



**Fig. 2** Distribution of RLP releases in Ciudad Real, Spain. **a** Total releases per ha (across the 15 study years 2002–2016). **b** Distribution of hunting estates (H.E.) by category (intensive vs non-intensive)

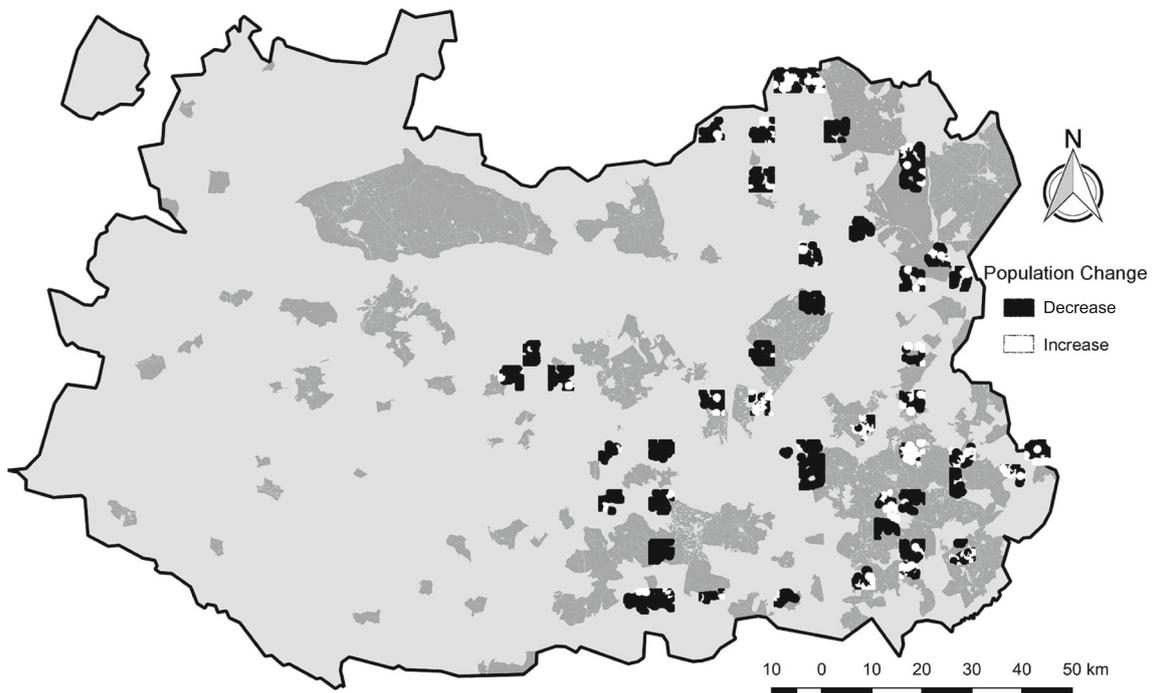


**Fig. 3** Effect of sampling date and hour on the number of male little bustards detected within 250 m of a sampling point. Estimated number of little bustards with 95% credible intervals for each 10 day-period (left) or each hour (right)

### Relationship between releases and little bustard population change

Our GLMM model showed a significant interaction between year and hunting area categories explaining little bustard abundance ( $X^2_4 = 13.28, P < 0.01$ ), as well as a significant interaction between longitude and latitude squared ( $X^2_1 = 4.74, P < 0.05$ ). According to our data, little bustard density in 2005 was similar in all types of hunting areas (Fig. 5). In

2016, little bustard abundance decreased significantly in all categories except in hunting estates with high intensity of releases ( $t_{345} = 1.36, P = 0.94$ ) (Fig. 5). The level of decrease was greatest in medium-intensity hunting estates (54%;  $t_{345} = 3.32, P < 0.05$ ) and non-hunting areas (52%;  $t_{345} = 5.59, P < 0.001$ ) (Fig. 5). In low-intensity hunting estates and hunting estates without releases, the level of decrease was less (34%;  $t_{345} = 3.77, P < 0.01$  and 29%;  $t_{345} = 6.54, P < 0.001$  respectively).



**Fig. 4** Spatial distribution of little bustard population change during 2005–2016 in Ciudad Real, Spain. Decrease is defined as values of the ratio between 2016/2005 abundances smaller than 0, increase as values higher than 0. The hunting estates with RLP releases are represented in dark grey

**Table 1** Statistical results of GLM test for the spatial analysis of little bustard population change during 2005–2016 in Ciudad Real, Spain

Variable	LR chi square	Df	P	Estimate	SE
X	23.62	1	< 0.001	0.09	0.019
Y	2.01	1	0.16	- 0.02	0.014
Y <sup>2</sup>	13.27	1	< 0.001	0.05	0.012
X*Y	0.10	1	0.75	0.01	0.018
X*Y <sup>2</sup>	3.71	1	0.05	- 0.03	0.017

X longitude, Y latitude

## Discussion

### Spatial and temporal patterns of red-legged partridge releases

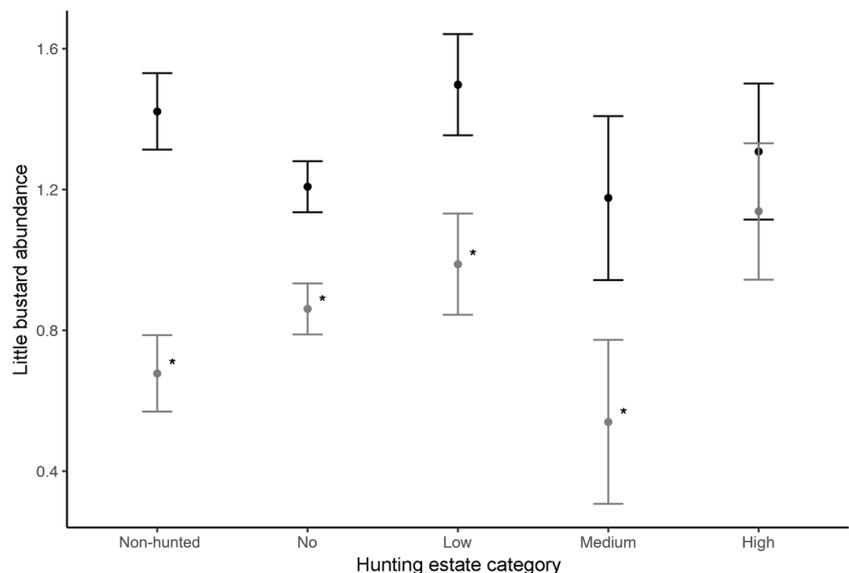
Official release data in Ciudad Real showed a large increase in the use of this management practice during 2002–2008. This trend reversed after 2008, probably because of the economic crisis (Fernández-Albertos et al. 2013; Caro et al. 2014; Rahman et al. 2017), which seemed to affect differently non-intensive and intensive estates. Some non-intensive estates continued releasing the same number of RLPs, but many others decided to stop releasing. By contrast, all intensive estates continued releasing, but reduced the numbers of partridges per release. Intensive estates are more profitable (Arroyo et al. 2017), potentially more resilient to financial problems, and may have opted for releasing less instead of stopping releases. Non-intensive hunting estates do not increase their profitability through releasing (Arroyo et al. 2017), and hence, when facing economic problems, they may have decided to stop releasing completely. The decrease

in the use of this management practice lasted until 2013 on intensive hunting estates. In more recent years, coinciding with the end of the worst years of the economic crisis in Spain, 2008–2013 (Rahman et al. 2017), the number of released RLPs increased again. This shows the importance that these hunting estates give to releases, with the numbers released increasing as soon as the economic climate was again favourable.

According to official data, around 600,000 RLPs were released annually between 2008 and 2012, although these official numbers are probably underestimates. In the province, a total of 575 out of the 1370 (42%) hunting estates had written into their Hunting Technical Plans the intention of releasing partridges (Ríos-Saldaña 2010), but only 29% of these (n = 165, representing 12% of the total) made an official request in at least 1 year by 2016. Estates whose Technical Hunting Plans allow them to request releases may (and do) choose not to release in 1 or more years. However, the discrepancy in figures may also indicate that some estates have not requested the annual authorisation, particularly if they are non-intensive and release small number of birds (see also Caro et al. 2014). In a study that interviewed 51 game managers of non-intensive estates (randomly chosen) from the same area, 35% of them declared having performed releases in the previous years (Arroyo et al. 2012), a percentage more similar to that coming from the Technical Hunting Plans than that arising from the annual official requests to release.

RLP releases were concentrated in certain areas, mainly in the south-eastern part of the province. This spatial pattern suggests that the releases done by a given hunting estate may be somehow conditioned by the releases done by neighbouring hunting estates, something that has been

**Fig. 5** Mean ( $\pm$  SE) abundance of breeding male little bustards (log-transformed;  $\text{Ln}(N/\text{km}^2 + 1)$ ) in each type of hunting estate and survey year (2005, black and 2016, grey). \* $P < 0.05$ . “Non-hunted” indicates non-hunting areas; “No” indicates hunting estates without releases; “Low”, “Medium” and “High” refer to hunting states with low, medium or high release intensity



suggested in interviews with game managers (BA, unpubl. data). In any case, our results indicate that partridge releases are substantial not only in terms of number but also in terms of their spatial extent, occurring on at least 20% of the area of Ciudad Real province.

### Changes in little bustard abundance and its relationship with release intensity

The Spanish little bustard population, the largest in Western Europe (García de la Morena et al. 2006), has suffered a 48% population reduction in 11 years (García de la Morena et al. 2018). These population decreases varied among Spanish regions, with Castilla-La Mancha, which includes the Ciudad Real province, still holding 60% of the Spanish population (García de la Morena et al. 2018). Despite this, our results showed that in Ciudad Real, little bustard population has also paired a strong decline, finding a difference of 46% between the counts of 2005 and 2016. Taking into account the credible interval of this estimate (31–61%), it is similar in magnitude to the value of 37% estimated by García de la Morena et al. (2018). Population decreases were more pronounced in the west than in the east of the province, and less pronounced in the north and south than in the longitudinal centre of the province. This spatial distribution could be explained, at least in part, by the social dynamics of the species. As a lekking species with strong conspecific attraction (Jiguet et al. 2000, Morales et al. 2014), the overall decrease may have prompted individuals from resultant low-density areas to move to remaining high-density areas such as the south-east of the province, following the mechanism proposed by Inchausti and Bretagnolle (2005). Whatever the mechanism, it is notable that little bustard populations decreased less (or concentrated themselves) in the south-eastern part of the province, just where the most intensive RLP releasing was conducted.

This result was also found at the scale of hunting estates categorised in terms of releasing intensity: the only areas where little bustard densities had not significantly changed were on hunting estates with the highest releasing intensity. This suggests that there may be factors that positively affect the little bustard on this type of hunting estate. Such factors may be related to habitat management or other forms of management, such as the provision of food and water or predator control (Draycott et al. 2008; Fletcher et al. 2010; Smith et al. 2010). We did not collect data about habitat quality or quantity, but other studies have shown that some management practices used by hunting estates making frequent releases may benefit other species (Draycott et al. 2008; Estrada et al. 2015). Among those, predator control and the provision of game crops (crops planted specifically for game that are not harvested) are

probably the most potentially beneficial for little bustards (Estrada et al. 2015), and these practices are significantly more frequent on hunting estates with high-intensity releasing (Arroyo et al. 2012). This is a plausible hypothesis that could explain why little bustards have decreased throughout the province except on hunting estates with high-intensity releases, and further study is required to verify it. The fact that breeding little bustards have not decreased in these areas is perhaps unexpected, given that hunting activity is a source of disturbance and affects the behaviour of this species (Casas et al. 2009; Tarjuelo et al. 2015), and in autumn, hunting activity is very intensive. We note that we have worked with breeding male data, and thus, we have no information on the changes in numbers of females and young, and their response to hunting management. Nevertheless, management practices such as game crops and predator control should also be beneficial for females and their offspring (Morales et al. 2013; Tarjuelo et al. 2013).

Neither our study design nor our results allow us to support or refute the hypothesis of an indirect impact of releases on wild little bustards through the transmission of parasites. This impact could be masked by hunting management factors (e.g. predator control or habitat management), compensating for the detrimental effects of parasite transmission or making the area more attractive for little bustards. If the latter occurs and parasite transmission takes place more strongly on these estates than elsewhere (owing to higher densities), it is possible that they may be functioning to some extent as ecological traps.

In summary, our results confirm a substantial difference in little bustard counts between 2005 and 2016, a negative population change of little bustards within the species' Spanish stronghold that was observed in the last national survey (García de La Morena et al. 2018). They also show the magnitude of RLP releasing for hunting in the region, but failed to detect any negative relationship between releasing and little bustard population change. This study raises several questions for future studies to address. In particular, it is crucial to little bustard conservation to understand the mechanisms by which management of hunting estates with high-intensity releasing may facilitate the persistence of male little bustards and to assess whether such management also benefits females and young. Also, given the large spatial overlap between areas with little bustards and those with high-intensity releasing, future work should establish whether parasites transfer from released RLPs to little bustards, and with what consequences. Meanwhile, the evidence presented here and from the literature suggests that at least some of the package of management measures carried out on intensive shooting estates could be useful for little bustard conservation. It would be important to identify which ones are beneficial to encourage them elsewhere.

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