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ORIGINAL ARTICLE

Improving decision-making for sustainable hunting: regulatory mechanisms of hunting pressure in red-legged partridge

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Abstract Knowledge about how hunting pressure is determined, and the relative efficacy of different mechanisms to regulate harvest, can help to improve the managers' decision-making process. We developed a general framework about the decision-making process that regulates red-legged partridge (*Alectoris rufa*) hunting pressure in central Spain based on information from a focus group and individual interviews with game managers. We also used available information to compare the efficiency of different tools thus improving some decision steps. We evaluated the cost-effectiveness of different population monitoring methods as a way to reduce uncertainty on partridge availability to hunters. Additionally, we investigated the relationship between annual harvest and various regulatory mechanisms of partridge hunting pressure used in the study area to identify the most potentially useful one to limit annual take-off. Game managers usually set hunting pressure after a qualitative assessment on population abundance prior to the hunting season, but this decision was frequently modified during the course of the hunting season according to variations in catch or perceived abundance at that time. Our results showed that kilometric abundance indices (counting partridges from cars along line transects) was a simple cost-efficient and reliable estimate of partridge density (estimated by Distance sampling). A variety of regulatory mechanisms were used by managers. The variables that most affected annual harvest (in addition to partridge abundance) were the number of driven-shooting days, and hunter density in walked-up hunting days, suggesting that their adjustment will be the most efficient regulatory mechanisms. We conclude that adequate monitoring on population abundance should be a critical step for managers' decision-making, and that a better understanding of the relative value of regulatory mechanisms, combining social and ecological approaches, would help improving our understanding of any human-mediated system, thus leading to better management recommendations.

Keywords *Alectoris rufa* · Distance sampling · Focus group · Game management · Harvest · Renewable resource

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Introduction

The sustainable use of renewable resources has become an explicitly stated goal of governments, managers and stakeholders, particularly after the Earth Summit declaration included it as a key part of sustainable development (UN 1992). Sustainable use of renewable resources is possible if rates of use do not exceed rates of regeneration (Daly 1991; Lande et al. 1997; Weinbaum et al. 2013).

Management that includes regulatory mechanisms of resource use has therefore the potential to avoid overexploitation (Sutherland 2001; Aanes et al. 2002). However, in practice, management tactics have often focused on maximizing short-term yield and economic gain, rather than long-term ecological sustainability (Christensen et al. 1996). Ecological monitoring is essential in the context of sustainable use because it provides crucial information on the state of the resource and the effectiveness of management actions (Sinclair et al. 2000; Bunnefeld et al. 2011), but accurate monitoring is costly and unattainable at times (Kinahan and Bunnefeld 2012). Uncertainty and imperfect knowledge may lead to wrong decisions and ultimately inefficient management and a loss of biodiversity (Milner-Gulland 2011). Given that resources for management and ecological monitoring are often limited, prioritization and evaluation of cost-efficiency of management and monitoring activities is particularly important (Caughlan and Oakley 2001).

A good example of renewable resources is game species. Although humans have hunted wildlife for millennia, increasing human populations, improved hunting technologies and growing commercial interests have contributed to increase pressure on wildlife populations. In fact, overhunting is currently considered one of the major threats to wildlife (Keane et al. 2005; BirdLife International 2012; Weinbaum et al. 2013). Sustained hunting demands despite declining trends in some game species will undoubtedly require more intensive and wiser management to support hunters' needs in a sustainable way. Indeed, some game managers increasingly use different management measures to boost wild game populations and harvest, like game birds (Oldfield et al. 2003; Draycott et al. 2007), as well as mechanisms to regulate harvest in an effort to make this practice sustainable (Taylor and Dunstone 1996; Sinclair et al. 2006).

As with other renewable resources, game management decisions are most likely to achieve their objectives if they are based on evidence and accurate information. They are, however, sometimes based on other factors, like perceptions or attitudes (e.g. Delibes-Mateos et al. 2013), or taken facing uncertainty or incomplete information (Bischof et al. 2012). For example, the level of uncertainty about true population size is frequently high, even when considerable resources are invested (Buckland et al. 1993; Norvell et al. 2003), and this uncertainty influences the population outcomes of harvest levels in the long term (Brooke and Tschapka 2002; Strand et al. 2012; Nuno et al. 2013). Additionally, and despite their potential importance to allow sustainability of game hunting, the relative efficacy of different mechanisms (e.g. adjusting the number of hunters per day or number of hunting days, variable hunting quotas, etc.) to regulate harvest has received less attention in the literature than other management activities (e.g. Baines et al. 2004; Bicknell et al. 2010; Broseth et al. 2012; Mustin et al. 2012), especially in Mediterranean countries. In this context, understanding the decision-making process in game managers could be useful to identify areas of uncertainty, as well as decision steps that need further attention.

Red-legged partridge (*Alectoris rufa*) hunting is an important economic activity in many areas of western Europe (Beja et al. 2009; Bicknell et al. 2010; Díaz-Fernández et al. 2012). Its populations have declined markedly over recent decades (BirdLife International 2012). In Spain, which holds 77 % of the world population, partridge decline has been attributed to changes in agricultural practices and overhunting (Blanco-Aguiar et al. 2004; Díaz-Fernández et al. 2013). Following this decline, the use of different game management tools (including regulatory mechanisms of hunting pressure) to increase partridge populations has become very frequent in Spain (Ríos-Saldaña 2010). However, a mismatch between abundance and take still happens in many estates, which leads to lower densities (Díaz-Fernández et al. 2013), suggesting that harvest decisions are not optimal.

The main aim of this study was to improve our understanding of managers' decision-making processes, and to evaluate the efficiency of different tools potentially improving some decision steps, in order to support sustainable use of red-legged partridges. Our partial objectives included: (1) to develop a general framework to explore the decision-making process that regulates partridge hunting pressure in central Spain, one of the main regions for small game hunting in the Iberian Peninsula (Ríos-Saldaña 2010); (2) to evaluate the most cost-efficient monitoring method among those frequently used in the scientific literature to estimate partridge abundance, as a way to reduce uncertainty on partridge availability to hunters; (3) to assess the relationship between some of the main regulatory mechanisms of partridge hunting pressure used in the study area and partridge harvest, thus their relative efficacy in regulating captures. We discuss the value of doing better monitoring and implementing more efficient regulatory mechanisms for the ecological and socio-economic sustainability of exploitation of renewable resources.

Materials and methods

Study area and context

The study area is located in central Spain (latitudes ranging from 37.98N to 40.33N and longitudes from 6.48W to 2.11W), which encompasses Spain's most productive hunting lands both historically and currently (Macaulay et al. 2013). Landscapes are dominated by open areas with different proportions of cultivated land and natural vegetation (mainly Mediterranean scrub). Small game hunting is both socially and economically important here (Garrido 2012), where >80 % of the territory is covered by hunting estates (Ríos-Saldaña 2010). Red-legged partridges are the main game bird species (Arroyo et al. 2012). There have been a number of studies in this study area that provide useful information to explore aspects related to hunting decision-making process (e.g. Ríos-Saldaña 2010; Arroyo et al. 2012; Díaz-Fernández 2012; Díaz-Fernández et al. 2012).

The general hunting season in the study area runs from early October to late February, closing before the onset of the partridge breeding season. The main methods used to hunt red-legged partridges are walked-up and driven shooting (Ríos-Saldaña 2010). In driven shooting, assistants beat the land to flush partridges and drive them towards a strategically arranged line of hunters. In walked-up shooting, hunters (with or without dogs) shoot the partridges as they encounter them (Barbosa et al. 2004).

General framework of decision-making process and regulatory mechanisms of hunting pressure

We aimed to capture a general picture of the decision-making process of partridge hunting pressure, rather than to present a complete and statistically representative reflection of different management options within the study area. To do so, we collected qualitative information through a focus group (including six people) and individual semi-structured interviews ($n = 10$) with small game managers. Such exploratory methodology is increasingly used to assess environmental phenomena in depth (e.g. Fischer and Young 2007). Collection of these data took place in 2012. Managers were selected from a database of hunting estates that had previously collaborated with our institute (Delibes-Mateos et al. 2013).

The discussion group and unstructured interviews generally started with a broad question about how partridge hunting pressure was decided, then focusing about when decisions were made and how partridge abundance (i.e. availability) was estimated. The last part of the discussion was usually dedicated to exploring the mechanisms used to regulate hunting pressure. Interviews and focus group were facilitated or carried out by JC and MDM. Discussions were transcribed, and we used a descriptive method frequently employed to interpret textual data (e.g. Schüttler et al. 2011). This consisted of an iterative process that started with the identification of the main issues such as when the decisions were made, which regulatory mechanisms were used or how population abundance was estimated. This provided the foundations to build the general framework. After that, we identified different options (e.g. different regulatory mechanisms) within the main categories, which provided a picture of the diversity of management options. In order to reinforce the discursive nature of this part of the paper, we have included a S1 in Electronic Supplementary Material showing literal quotations from discussions (Oñate and Peco 2005; hereafter we refer to each quotation as Qni where ni is the specific number in the S1).

Partridge abundance estimates

In order to evaluate the efficacy of different partridge abundance estimating methods, which could lead to recommendations about how to reduce uncertainty of partridge availability for harvest decisions, we used data from field surveys carried out in summer (between cereal harvesting and mid-August) 2004–2005 and 2008–2012. Therefore, our partridge abundance estimates related to annual maximum abundance, i.e. after the breeding season and before the hunting season. Surveys were based on both point count and line transect methods, as these are the main ones used in the scientific literature (e.g. Borralho et al. 1996; Buenestado et al. 2009; Díaz-Fernández et al. 2013). They were carried out from sunrise to about 3 h later and the three last hours of the day, avoiding the hottest central hours, when activity is lowest (Ricci 1989), and adverse weather conditions (Bibby et al. 2000). Using binoculars, observers counted partridges during 10 min in points situated along tracks and distant 700–750 m from each other. Distance between observer and each partridge observed was visually estimated. Intervals between points were driven at a constant speed (around 20 km/h), and all partridges observed from the car during these transects were noted. Partridges observed were categorized according to whether they were alone, in pairs or in 'clusters' (>2 partridges). From that information, we calculated the following abundance estimates:

Partridge density

We calculated partridge density estimates using Distance sampling 6.0 software (Thomas et al. 2010) and observations obtained in point counts (where distance to partridges observed was noted). We used this value as the reference method, as it represents the most accurate scenario of true population abundance (Thomas et al. 2010; Fernandez de Simon et al. 2011). Multiple covariate distance sampling (MCDS) was used to examine the effect of habitat type and observer on the detectability of animals (Diefenbach et al. 2003; Marques et al. 2007). To create the detection function a minimum number of observations in each estate is required and abundance estimates of partridges showing a coefficient of variation higher than 40 % were not considered (Gottschalk and Huettmann 2010). Sample size for comparisons thus was $n = 32$. See S2 for more details.

Kilometric abundance indices (KAIs)

We estimated KAI as total number of partridges observed during transects divided by total kilometres driven in an estate (Borralho et al. 1996). Additionally, we divided the number of cluster during transects by the total km driven (cluster/km). In three game estates KAIs were not assessed. On average, 58.3 ± 51.9 (SD) km (range 13.0–276.5, $n = 30$) of line transects were driven in each estate.

Indices from partridge observations in points

We assessed partridge/point as total partridges observed during point counts divided by the total number of points monitored in an estate (Díaz-Fernández et al. 2012). On average, 76.7 ± 72.5 SD (range 20–424, $n = 32$) points were monitored per estate. Additionally, we calculated the number of clusters observed in point counts divided by total number of points monitored (cluster/point) and percentage of points with at least one contact (% positive points).

Average cluster size

We also calculated the average size of clusters observed during transects and for clusters observed during point counts, as this related to an estimate sometimes used by managers (see results).

Finally, we estimated the relative cost of each method tested. In order to do this, we implemented each method in five estates during summer 2013, and we calculated the average time and fuel expenditure needed for censusing an area of 10 km^2.

Effect of regulatory mechanisms on partridge harvest

To assess the effect of different regulatory mechanisms on partridge harvest, we used information from a database of 59 game estates in central Spain, gathered through face-to-face interviews with game managers in 2005 and 2008–2010 within previous projects (see for more details Arroyo et al. 2012; Delibes-Mateos et al. 2013). In this study, we used information on estate size, the number of partridges harvested in the study season, the number of walked-up and driven-shooting days in that season (hunting days), as well as average number of hunters participating each hunting day in both hunting methods. We calculated harvest per area and hunter density by dividing annual harvest and number of hunters per hunting day by the estate surface to obtain comparable figures among estates (Table S3.1). We also considered whether there were hunting quotas (a binomial variable, yes or no, as we did not have information to identify the type of quota), and whether there was any spatial limitation of hunting (either through hunt-free reserves, or through dividing the estate in several sections and hunting each section in different days, see results). This latter variable had five ordinal values, from 1 (no spatial regulation) to 5 (at least 10 % of the estate was hunt-free or there was higher spatial division of hunting days). As harvest should be related to abundance (Willebrand et al. 2011 and references therein), we also included in the analyses an estimate of abundance in those estates based on field observations (see above). We used partridges/point, as this estimate had the best fit in relation to density (see results). We did not use partridge density because we could not calculate this variable for several of the study estates with management information (see S2). We obtained information on all of these variables (regulatory mechanisms as well as abundance) for a total of 39 estates.

Statistical analyses

Relationships between partridge density (distance sampling estimates from point count data) and other abundance indices were examined with linear regressions with the R-function lm (library stats; R development Core Team 2013). We used non-linear distributions when higher r^2 were obtained (Sokal and Rohlf 2012).

The relationship between harvest and the different regulatory mechanisms used in hunting estates was modelled with General Linear Models, with the R-function glm (library car). We used harvest per area as response variable (normal distribution and identity link), and partridge abundance, number of walked-up hunting days, number of driven-shooting days, hunter density in walked-up shooting days, hunter density in driven-shooting days, existence of quotas, and spatial limitation of hunting as explanatory variables. Additionally, we considered the interaction between number of hunting days and hunter density for each hunting method, and the existence of quotas and number of walked-up hunting days (usually no quotas exist for driven shooting). We performed all possible combinations of these explanatory variables, as all of those models were plausible and we were interested in whether each regulatory mechanism alone or in combination with others could better explain annual harvest variation among estates. We did this with the function dredge (library MuMIn), selected the models with $\Delta AIC_c < 2$ (Burnham and Anderson 2002), and calculated model-averaged parameter estimates for the variables included in those models, as well as their relative importance (RVI), calculated as sum of Akaike weights across all the models in the set where that variable occurred (Burnham and Anderson 2002).

Results

General framework of decision-making process and regulatory mechanisms of hunting pressure

According to the interviewed managers or participants in our focus group, the decision-making process that regulates partridge hunting pressure in central Spain includes three important steps. First, managers agreed that partridge abundance is usually assessed in summer (Fig. 1a), after partridge reproduction. According to their comments, this assessment is rarely based on systematic surveys, rather usually made through personal observations (see Q1–2 in S1), or through qualitative information provided by other people (i.e. game-keepers, farmers, shepherds). Some managers mentioned that they based their harvest decision according to relative number of partridge chicks or cluster size observed in summer (Q3).

Second, there was a consensus among managers about the fact that hunting pressure should be regulated to make this activity sustainable (Q4). Most managers agreed that decision-making about hunting pressure takes place before the official start of the hunting season (around mid-October; Fig. 1a; see an example in Q5). Options vary from hunting without any self-regulation to banning hunting in low partridge abundance years (Fig. 1a). This latest is an extreme option that, according to the managers, rarely occurs.

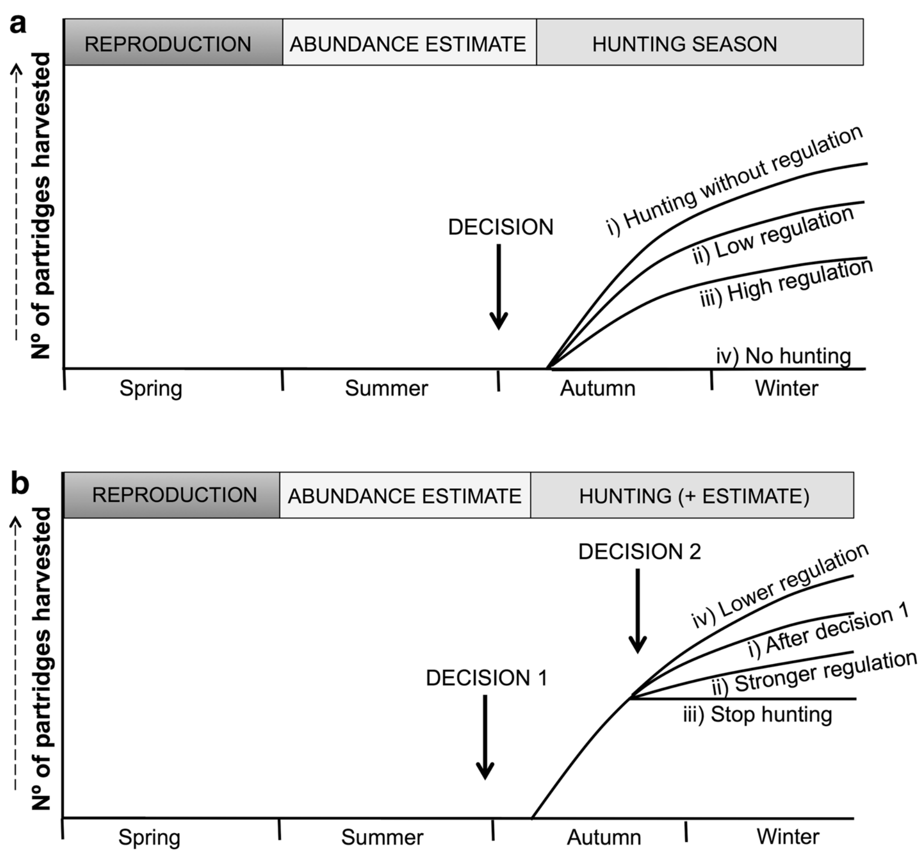

Fig. 1 General framework of the decision-making process of red-legged partridge hunting pressure. **a** A first decision is taken before the beginning of the hunting season and after population abundance assessment. The accumulated number of partridges harvested increases during the season, but the increase in the number of partridges harvested will be lower as the availability of partridges decreases during the season. Overall, the slope of the relationship between time and harvest will depend on partridge availability and hunting pressure in each specific estate. The number of partridges harvested will be higher if hunting pressure is not regulated (*i*); the stronger the regulation, the lower the total number of partridges harvested (*ii*, *iii*). In years of very low partridge abundance, the decision may consist of banning hunting (*iv*). **b** A second decision is usually taken during the hunting season. We show the evolution of partridges harvested that would happen after decision 1 (*i*) for comparisons. If hunters perceive partridge abundance during the hunting season is low, they can impose additional stronger regulations (*ii*), hence decreasing the total number of partridges harvested. Hunters may also decide to stop hunting during the season if partridge availability is very low (*iii*). On the contrary, hunters may also decide to increase hunting pressure (e.g. adding some extra days of hunting) if partridges are very abundant one given year (*iv*). See more details in the main text

Finally, participants declared that a second decision regarding hunting pressure regulation is frequently made during the course of the hunting season (Fig. 1b). According to statements, this decision may be based on the number of partridges harvested during the hunting season, the number of partridges flushed during the hunt, or even on the mood (degree of satisfaction) of the hunters at the end of the day (Fig. 1b and Q6–7). Thus, further hunting regulations can be imposed along the hunting season (Fig. 1b), for example shortening the season or even stopping it (see below). One manager also mentioned that hunting pressure can be exceptionally increased during the hunting season (Fig. 1b; e.g. organizing an extra driven-shooting day) if partridges are extremely abundant one given year.

With regard to regulatory mechanisms of hunting pressure, managers declared that limiting hunter numbers is commonly used. Nevertheless, it was acknowledged that this is a difficult task in some estates (Q8). Participants also commented that limitation of the number of hunting days is very common (Q9). This limitation can be done by starting hunting after the official date of opening the season (Q10), or finishing it before the official end of the season (Q11). Game managers declared that the number of hunting days is generally set before the start of the hunting season (decision 1; Fig. 1a), although it is frequently modified (e.g. shortening the season; see above) according to the evolution of harvesting (decision 2; Fig. 1b). In addition, some managers said a limitation of duration of hunting in a given day is usually self-imposed (Q12). An alternative frequent way of regulating pressure is limiting hunting spatially through establishing hunting-free reserves. However, most managers acknowledged that free-hunting reserves are established just because these are imposed by law (Q13). Furthermore, managers mentioned that setting hunting quotas (limiting the number of partridges to be shot per hunter and day) is also frequently used. Managers also pointed out that quotas are usually fixed before the start of the hunting season (decision 1; Fig. 1a), but can be adjusted during the season (decision 2; Fig. 1b). Game managers also commented that quotas are very variable among estates, and actively discussed about their usefulness (see examples of opposing views in Q14–15). Finally, it was briefly stated in the focus group that another potential way of regulating hunting pressure is through modulating the use of different methods to hunt partridges; for example, organizing an extra driven-shooting day those years in which partridge abundance is higher.

Partridge abundance estimates

All our abundance estimates except average cluster size were significantly and positively correlated with partridge density (Table 1; Fig. 2). Among estimates, the number of partridges per observation point showed the best fit in relation to the reference method, although the relationship with KAI and cluster/km was also very high (Table 1). Time needed to census 10 km^2 was around half as low in line transect methods than observation point methods (65.33 $\pm$ 13.29 SD and 129 $\pm$ 8.88 SD min, respectively). Similarly, line transect methods had lower fuel costs (4.87 $\pm$ 1.51 SD L) than observation point methods (5.89 $\pm$ 2.84 SD L). Presence/point had time cost of 102 $\pm$ 22.31 (SD) min (22.31 SD) and fuel cost of 5.89 $\pm$ 2.84 (SD) L. Line transects were thus more cost efficient.

Relationship between harvest and regulatory mechanisms

The variables that best explained variation in harvest per area among hunting estates were number of driven-shooting days over the season, density of hunters in walked-up hunting days, partridge abundance and density of hunters in driven-shooting days (Table 2 and Table S3.2). Of these, the first three were the ones with highest relative importance and harvest per area was positively related to all of them (Table 2). Additionally, harvest per area was lower in those estates where the density of hunters in driven-shooting days was higher (Table 2). Only nine studied estates offered driven-shooting days (between 2 and 13 days per hunting season). Analyses carried out excluding these estates showed that the best variables explaining variation in harvest per area were density of hunters in walked-up shooting days (RVI = 0.77) and partridge abundance (RVI = 0.72). No detectable effect of hunting quotas and spatial limitation of hunting was found.

Discussion

Better monitoring for sustainable harvest

Game managers in our study acknowledged that harvest regulations are essential to mitigate current red-legged partridge population decline, and thus maintain sustainable hunting bags. In this regard, a critical premise for efficient regulation mechanisms is to acquire reliable data on population size, based on adequate monitoring (Sutherland 2001; Freckleton et al. 2006; Msoffe et al. 2009; Jakob et al. 2014). Managers and scientists often rely on indices of population size (e.g. indirect information) that may be more or less tightly correlated with true population size (Solberg and Sæther 1999; Fernandez de Simon et al. 2011; Strand et al. 2012). According to our findings, managers in our study estimate relative partridge abundance using qualitative information, instead of any repeatable (and

Table 1 Regression analyses between partridge density, obtained by Distance sampling, and the abundance obtained by different methods to estimate partridge abundance

Abundance estimates	*n*	R^2	*P* value	Adjusted regression
Partridges/point	32	0.959	<0.0001	Linear
KAI	29	0.924	<0.0001	Linear
Clusters/point	32	0.941	<0.0001	Linear
Clusters/km	29	0.923	<0.0001	Linear
Average cluster size/point	32	0.263	0.004	Exponential
Average cluster size/km	29	0.012	0.56	Logarithmic
Presence/point	32	0.758	<0.0001	Exponential

Table 2 Model-averaged estimates and relative variable importance (RVI) of the variables included in the best (<2 ΔAIC_c) models explaining variations in harvest per area (partridges hunted yearly per km^2)

Variables	Parameter estimates ± SE	RVI
Walked-up shooting hunter density	8.43 ± 3.32	1.00
Driven-shooting days	7.31 ± 2.11	1.00
Partridge abundance	3.58 ± 1.77	0.78
Driven-shooting hunter density	−4.16 ± 3.03	0.48

Models are shown in Table S3.2

comparable) methodology, which is likely associated with a higher degree of error and uncertainty about true population size. An increasing number of studies highlight the effects of uncertainty of wildlife survey monitoring data on the predicted consequences of different harvest scenarios (Bunnefeld et al. 2009; Holland 2010; Nuno et al. 2013). This means that current red-legged partridge harvest decisions will lead to under-harvesting or over-harvesting, both of which have potential negative consequences (economically and ecologically, respectively; see also Díaz-Fernández et al. 2012, 2013).

Unfortunately, it was not possible in our study to assess the exact magnitude of the error associated with managers' estimates, since we did not have manager's estimates for the studied localities while we executed field surveys. Studies evaluating this would be critical to assess whether and when managers under- or overestimate partridge population size, and thus predict the population consequences of management decisions. In any case, some of the indices used by managers to estimate abundance (e.g. cluster size) were not related to density, so errors could be high. The fact that decisions about hunting pressure are frequently modified during the hunting season (according to temporal variations in harvest), even in estates where abundance have been previously estimated, also suggests that initial abundance estimates is insufficiently accurate to allow appropriate regulation decisions. In any case, other factors like high mortality rate due, for example, to disease outbreaks (Gamino et al. 2012) after initial abundance estimates, could also play an important role in the modification of initial hunting pressure.

Our results also showed that counting partridges or clusters in car-driven line transects is a cost-effective reliable method to estimate population size, as previously suggested by other authors (Ricci 1989; Borralho et al. 1996). Implementing this simple population assessment may thus enable to improve the decision-making on hunting pressure for a sustainable harvest of red-legged partridges. Further studies should, however, evaluate whether accuracy of population estimates based on KAI holds at lower partridge densities. This is important as partridge densities observed in a few of our study estates (Fig. 2) were very high as compared with other areas in the Iberian Peninsula (e.g. Borralho et al. 1996; Duarte and Vargas 2001; Buenestado et al. 2009), because they may have released farm-bred partridges in early summer (see Díaz-Fernández et al. 2013).

Improving regulatory mechanisms

In our study, we observed that hunting pressure had higher relative importance explaining variations in annual harvest in hunting estates than variations in partridge abundance. Similar results have been reported for willow grouse (*Lagopus lagopus*) in northern Europe (Willebrand et al. 2011). These results highlight the potential of appropriate regulatory mechanisms to avoid over-harvesting, thus leading to sustainable (or even increasing) game species populations (Willebrand and Hörnell 2001; Aanes et al. 2002; Willebrand et al. 2011).

Regulatory mechanisms identified in this study included limiting the number of hunting days or hunter density,

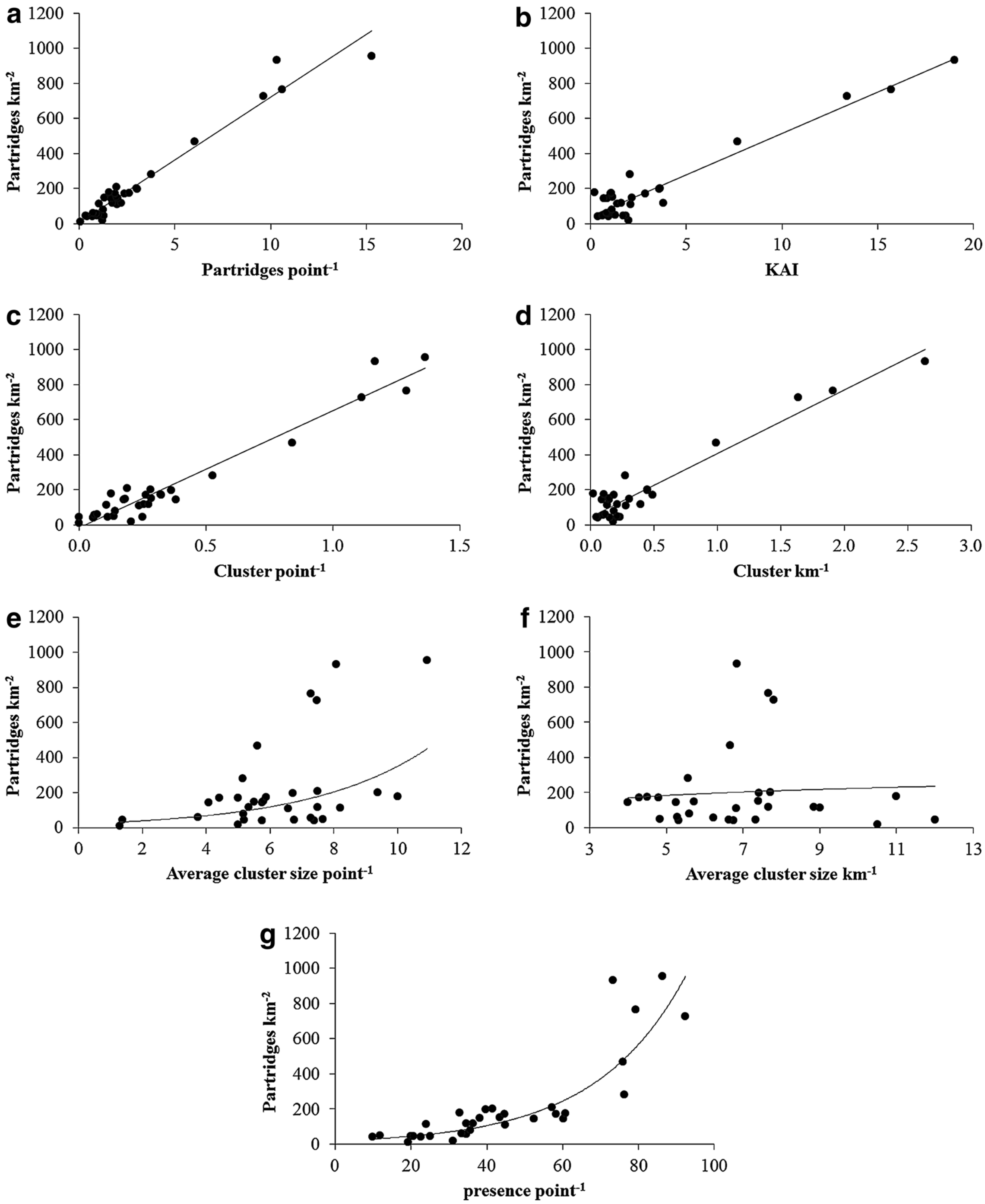

Fig. 2 Relationships between partridge density estimates by distance sampling (reference method) and other estimating methods of abundance (**a**–**f**). Trend line is presented (see also Table 1)

setting hunting quotas (as a limit to the number of animals shot per hunter and hunting day), and other mechanisms like limiting hunting spatially or regulating the frequency of different hunting methods. Regulatory mechanisms in central Spain are thus similar to those used for other game species in other areas (Taylor and Dunstone 1996; Calvert and Gauthier 2005; Broseth et al. 2012; Wam et al. 2013). Assessments of different regulatory mechanisms allow determining the optimal implementation of harvest regulations (Conroy et al. 2002; Willebrand et al. 2011; Wam et al. 2013). Our results indicate that for red-legged partridge estates, modifying the number of driven-shooting days or hunter density in walked-up shooting days has the highest likelihood of modifying total take-off in the estate over the hunting season and would thus be the most effective tools to be used to regulate harvest. The negative relationship found between partridge harvest and driven-shooting hunter density after taking into account number of driven-shooting days probably reflects that driven-shooting days offered in non-commercial hunting estates are attended by a large number of hunters, but lead to smaller harvest, whereas commercial estates offering driven-shooting days usually limit the number of hunters to obtain higher prices. In any case, this variable had a low relative importance explaining harvest per area.

Interestingly, harvest was unrelated to number of walked-up hunting days (even in interaction with hunter density), although modifying number of hunting days over the season is frequently applied according to manager's comments. Similarly, variables, like the existence of daily quotas or spatial limiting of hunting, did not have a significant relation to annual harvest. The latter may be related to the coarseness of the variables as used in our analyses, but this suggests that managers are using tools for regulating hunting that are inefficient, as they do not necessarily lead to lower harvest. In fact, hunting daily quotas were applied in 62 % of estates sampled, while average spatial limitation affected <10 % of estate area (Table S3.2), thus in many estates these regulatory mechanisms seem to be poor.

Conclusions

In contrast to the view that mortality through hunting is mostly compensatory (Andersen 2008), it is now widely recognized that harvesting may alter the abundance and population dynamics of game species (Solberg et al. 1999; Weinbaum et al. 2013). Game species thus require a dynamic and adaptive harvest management strategy (Broseth et al. 2012), due to large interannual variation in demographic rates, such as recruitment and survival (Watson and Moss 2008; Delibes-Mateos et al. 2009; Martínez-Padilla et al. 2014). Our work supports the notion that improving monitoring (leading to better knowledge of population abundance before the hunting season) will in turn lead to better management decisions (i.e. better adjustment of hunting pressure to abundance; Aanes et al. 2002). Additionally, it highlights that a high proportion of managers are currently using inadequate tools to regulate harvest, as they do not necessarily lead to overall lower catches, which may have unwanted population consequences and may contribute to explain the decline this species is suffering (Blanco-Aguiar et al. 2004; BirdLife International 2012). On the other hand, it is important to remember that the discrepancy between harvest intentions by managers and how harvest is performed can be substantial (Bischof et al. 2012 and reference therein). Further studies should therefore also investigate hunters' preferences for different regulatory mechanisms (Andersen 2008), so long-term consequences of these on populations and estate sustainability can be fully evaluated.

More broadly, our study example reminds that a good understanding of any human-mediated ecological system needs a combination of both ecological and social approaches, including studies on factors influencing management or market decisions, on the relative efficacy of different management options and also, as mentioned above, on uncertainty when implementing rules and regulations (i.e., factors affecting behaviour of the end-user, in this case hunters). This broader approach will lead to management recommendations ecologically more efficient and more to be implemented as appropriate.

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