

Effects of hunting on the behaviour and spatial distribution of farmland birds: importance of hunting-free refuges in agricultural areas

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Abstract

Hunting is one of the human activities that directly affect wildlife and has received increasing attention given its socioeconomic dimensions. Most studies have been conducted on coastal and wetland areas and showed that hunting activity can greatly affect bird behaviour and distribution. Hunting-free reserves for game species are zones where birds find an area of reduced disturbance. We evaluated the effect of hunting activities on the behaviour and use of hunting-free areas of lapwings *Vanellus vanellus*, golden plovers *Pluvialis apricaria* and little bustards *Tetrax tetrax* in agricultural areas. We compared the habitat use and behaviour of birds on days before, during and after hunting took place. All three studied species showed strong behavioural responses to hunting activities. Hunting activity increased flight probability and time spent vigilant (higher on hunting days than just before and after a hunting day), to the detriment of resting. We also found distributional (use of hunting-free reserve) responses to hunting activities, with hunting-free reserves being used more frequently during hunting days. Thus, reserves can mitigate the disturbance caused by hunting activities, benefiting threatened species in agricultural areas. Increasing the size or number of hunting-free areas might be an important management and conservation tool to reduce the impacts of hunting activities.

Introduction

Animals can perceive humans as potential predators and often alter their behaviour in the presence of people. The increase in human population and leisure activities has amplified the potential consequences of human disturbances on wildlife (Blanc *et al.*, 2006), including wild birds (Stockwell, Bateman & Berger, 1991; Madsen & Fox, 1995; Fox & Madsen, 1997; Bautista *et al.*, 2005; Arroyo & Razin, 2006). However, the overall effects of increasing human disturbance on bird populations are still poorly documented (Guillemain *et al.*, 2007), and there is often much debate about how human activities should be regulated (see e.g. González *et al.*, 2007 and references therein).

Hunting is one of the human activities that affect wildlife most, and it has received increasing attention given its environmental, social and economic dimensions, particularly in Europe (Lucio & Purroy, 1992; Martínez, Viñuela & Villafuerte, 2002). However, hunting activity can be compatible with a conservationist policy, promoting and financing preservation of natural ecosystems, in a context of 'wise use', whenever an adequate management plan is implemented, adjusting human traditional activities, hunting and

wildlife conservation (Lucio & Purroy, 1992; Tapper, 1999; Robinson & Bennett, 2004).

Most studies on the effect of hunting disturbance on birds have been conducted on coastal, wetland and forest birds, mainly focusing on game species (Madsen & Fox, 1995; Fox & Madsen, 1997; Bregnballe, Madsen & Rasmussen, 2004; Duriez *et al.*, 2005; Klaassen *et al.*, 2006; Stafford *et al.*, 2007; Thiel *et al.*, 2007; Thiollay, 2007). These studies have evidenced that hunting causes local disturbance effects on target game species, and may also affect other species of conservation concern (Madsen & Fox, 1995; Fox & Madsen, 1997; Madsen, 1998*b*). Nevertheless, the effects that hunting and game management have on non-target protected species are still poorly known (Arroyo & Beja, 2002). In a recent attempt to reduce the impact of hunting on wildlife, hunting reserves, where birds can benefit from reduced disturbance have been created in North America and in several European countries (e.g. Madsen, 1998*a,b*; Stafford *et al.*, 2007), but their efficiency as management tools has been poorly investigated yet (Duriez *et al.*, 2005). Refuge size, location and network structure must ensure that birds find all their biological requirements, reducing to a minimum external disturbance (Fox & Madsen, 1997).

Hunting activity is widespread in farmlands and agricultural habitats (Howard & Carroll, 2001; Martínez *et al.*, 2002), and is one of the main alternative options available to farmers in several European countries such as France, Spain or the UK, providing an added socioeconomic value in some rural areas (Bernabeu, 2000; Howard & Carroll, 2001; Martínez *et al.*, 2002). However, the effects of hunting on birds in these habitats remains little studied as compared with birds inhabiting other habitats, for example, aquatic. This is important because dramatic population declines have been reported in many bird species in agricultural habitats (Donald, Green & Heath, 2001; Robinson & Sutherland, 2002). Hence, hunting management programmes should aim to enhance the conservation of game birds together with that of the species that share the same habitat and ecological requirements, and should be integrated with agricultural management programmes (e.g. Jolivet *et al.*, 2007). There is a need for further research on the effects of hunting activities on key farmland bird species of conservation concern (Tucker & Heath, 1994).

Our aim here is to evaluate the effect of hunting activities on the behaviour and the use of hunting-free areas of birds that inhabit agricultural areas in western France. We focused on behaviours such as time spent flying, or vigilant to the detriment of feeding or resting, which might indicate indirect costs of hunting activities to farmland birds. We selected the northern lapwing *Vanellus vanellus* (hereafter 'lapwing'), the European golden plover *Pluvialis apricaria* (hereafter 'golden plover') and the little bustard (*Tetrax tetrax*) as model species. Golden plover and lapwing are classified as 'not globally threatened' (del Hoyo, Elliott & Sargatal, 1996) and are hunted in France. In contrast, the little bustard is fully protected since 1972; it is currently classified as 'Vulnerable' in Europe (Goriup, 1994) and 'Red-listed' in France (Rocamora & Yeatman-Berthelot, 1999). Farmland habitats in western France hold *c.* 80% of

the country's population of little bustards (Jolivet *et al.*, 2007), which has suffered dramatic declines in recent years (Morales, Bretagnolle & Arroyo, 2005; Jolivet *et al.*, 2007). In autumn, when the study was conducted, little bustards prepare for their southward migration (to Spain), while lapwings and golden plovers arrive for wintering on the study area.

We compared the use of hunting-free areas and the behaviour (time spent flying, vigilant, resting or foraging) of birds on days before hunting took place, during a hunting day and after a day of hunting. We predicted that birds would be more often disturbed during hunting days, and would spend more time flying and being vigilant, to the detriment of resting or foraging activities. We also predicted that birds would avoid areas where disturbance due to hunting activities take place, and use more often hunting-free areas when hunting takes place.

Materials and methods

Study area

We conducted this study in an intensively cultivated area (*c.* 10 km²) in south-western France (46°37'N, 0°2'W; Fig. 1) in autumn 2003 (2 October–6 December). This year, hunting season legally opened on 5 October, and hunting was conducted twice a week (on Thursdays and Sundays), by a variable number of hunters, from sunrise to sunset, with a break in the middle of the day. Hunters locally targeted small game mammals (lagomorphs) and game birds (Galliforms), showing less interest to lapwings and plovers. The hunting method used was walk-up shooting with dogs (usually one or two dogs for hunter, but sometimes up to six), the hunters forming an attacking line of three to six hunters, spaced every *c.* 40–50 m. Within the study area, hunting is permitted in some areas, but not in other, which

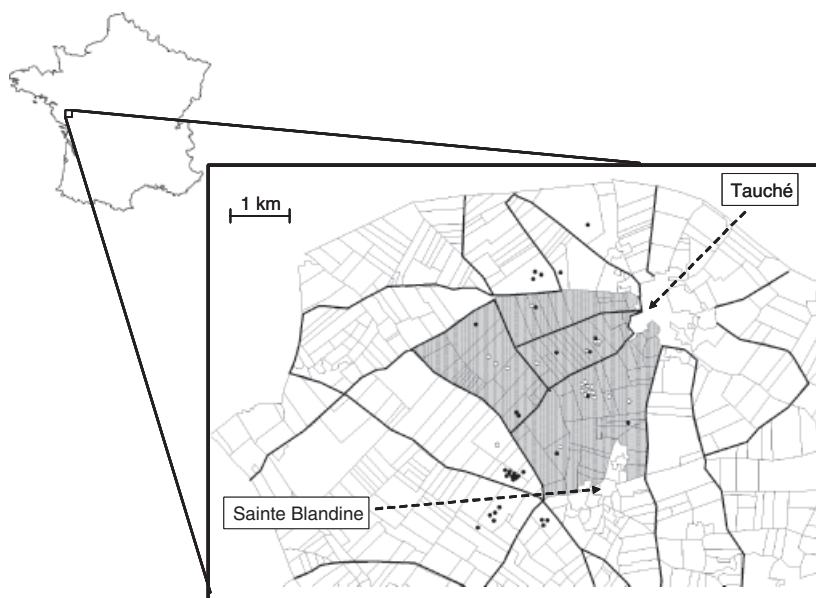


Figure 1 Location and map of the study area in western France (communes of Tauché and Sainte Blandine villages). In white, fields outside the reserve, in grey hunting-free area. Black lines are tracks or roads used for road transects (see 'Materials and methods'). The dots show the locations of lapwing *Vanellus vanellus* and golden plover *Pluvialis apricaria* mixed flocks during non-hunting days (black dots ●) and during hunting days (white dots ○).

are set by local hunters and act as wildlife reserves and are most often located near villages (see Fig. 1).

Data collection

Distribution, flock size and habitat use

We studied the distribution of focal species using road transects within the core area. Every 1–2 days, we systematically looked for and mapped individuals or flocks of the study species using always the same network of roads or tracks (Fig. 1). The observer drove at low speed (20 km h⁻¹) and stopped regularly to look for, identify and count birds using binoculars or a telescope. Observations were made from a distance such that birds were not disturbed during transects. For each observation, we recorded the date, time, exact location on a map, number of individuals of each species and the habitat used. The high density of transects within the study area gave us confidence of surveying correctly all the study area and detecting all flocks and most isolated individuals of the focal species.

Transects were conducted before the start of the hunting season in the core area, and on days before, during and after hunting took place. We began conducting transects every working day from sunrise until 11:00 (AM) and between 16:00 until sunset (PM). Transects were not conducted in the middle of the day, when birds were less active (pers. obs.; Roth & Lima, 2007 and references therein).

Behavioural observations

When a flock was located, we randomly selected an individual within it, and conducted a 60 s (± 1) focal sampling (see Altmann, 1974), using stop-watch and a tape recorder. Observations were conducted from the car, used as a hide, and birds always seemed unconcerned by the presence of the observer. After each focal sampling, we waited for 1–2 min before starting another focal sampling on another individual. Birds were not individually marked, but we selected another bird that was at least at 10 m from the previous focal one, and only watched it when we were confident that it was a different individual. The maximum number of individuals observed (focal sampling) in a given flock on a given day were 21, 26 and 22 individuals, in flocks of 68, 500 and 65 individuals of little bustard, lapwing and golden plover, respectively.

Recordings of behavioural observations were subsequently analysed to quantify the duration of each behaviour (time spent flying, vigilant, resting or foraging), which were defined and classified using prior experience and previous works describing the main behaviours of study species (Cramp & Simmons, 1980, 1983; Barnard, Thompson & Stephens, 1982; see also supporting information for a more detailed definition of behaviours). We did not carry out observations in bad weather conditions (windy, rainy or frosty days) and the semi-experimental design (observations before, during and after a hunting day, on repeated hunting days) allowed us to minimize the potentially confounding effects of changing weather conditions on bird behaviour.

For each observation, we also recorded the following data: sampling date (Julian date; 1 = 1st of October), time of day, subsequently allocated to one of two daytime periods (AM or PM) and flock size (number of birds in the group). Sample sizes for each species were as follows: little bustard: $n = 298$; lapwing: $n = 375$; golden plover: $n = 172$.

Statistical analysis

Effects of hunting on behaviour

The probability of a bird flying during a watch was fitted to models using a binomial error distribution and a logit function (logistic regression). The % time spent by focal birds in different behaviour (arcsin transformed) was fitted to models using a normal error distribution and an identity link function. Explanatory variables included the daytime period (AM vs. PM), the sampling date (Julian date), the group size and the hunting activity (three classes: day before hunting, day when hunting took place and day after hunting). We tested for non-linear relationships with sampling date or group size by including a quadratic term in the model (date²; group size²), and kept it in our models when significant ($P < 0.05$). When variation in behaviour was explained by hunting activity, we conducted pairwise comparisons between days before, during and after hunting took place.

Effects of hunting on the use of hunting-free areas

We tested whether the probability of a flock using a hunting-free area depended on hunting activity (comparing days before hunting day, hunting days and days after hunting). We fitted the variable 'reserve use' (birds inside or outside of hunting-free reserves) to the model using a binomial logistic model with log link function, and performed a χ^2 analysis on a contingency table with the variables 'reserve use' and 'hunting day'. To control for variations due to daytime period, date, habitat, flock size and hunting activity we included these as explanatory variables in the models. The significance of the effects was tested using the Wald statistic (test of significance of the regression coefficient).

Results

Hunting and behaviour

Flying

Variation in the occurrence of flights by little bustards was explained by daytime period (flights were observed only AM) and hunting activity (flights were observed only on hunting days; Table 1; Fig. 2), but not by sampling date or flock size.

For lapwings, flight probability during a watch was not significantly explained by sampling date, but was explained by daytime period (birds were more likely to fly PM than AM), flock size (quadratic function: flight occurrence decreased with increasing group size, but increased in larger groups,

Table 1 Effects of daytime period, date, group size and hunting activity on the behaviour of studied species

Behaviour	Source of variation	Little bustard			Lapwing			Golden plover		
		d.f.	χ^2	<i>P</i>	d.f.	χ^2	<i>P</i>	d.f.	χ^2	<i>P</i>
Flying probability	Daytime period	1290	9.57	0.039	1367	4.22	0.039	1166	11.32	<0.001
	Flock size				1367	6.08	0.014			
	Flock size ²				1367	16.72	<0.001			
	Hunting activity	2290	6.15	<0.001	2367	34.53	<0.001	2156	15.46	<0.001
		d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Vigilance	Daytime period	1283	5.53	0.019	1266	5.04	0.026			
	Date	1283	6.70	0.010	1266	4.11	0.044			
	Date ²	1283	6.91	0.009						
	Flock size	1283	3.49	0.063	1266	4.93	0.027			
	Hunting activity	2283	19.54	<0.001	2266	9.93	<0.001	2107	9.26	<0.001
Resting	Daytime period									
	Flock size	1283	4.57	0.033	1266	6.66	0.010			
	Flock size ²	1283	6.34	0.012						
	Hunting activity	2283	8.45	<0.001	1266	3.19	0.043	2107	6.57	0.002
Foraging	Daytime period				1266	5.04	0.026			
	Date				1266	7.70	0.006			
	Flock size	1283	15.37	<0.001						
	Flock size ²	1283	16.96	<0.001						
	Hunting activity	2283	0.37	0.693	1266	1.24	0.290	2107	0.38	0.684

Only the final models are presented. All initial models included daytime period (AM vs. PM), sampling date and sampling date², group size and group size² (to test for linear or quadratic relationships with date or group size) and hunting activity (day before, during or after hunting took place). Non-significant variables ($P=0.10$ level) were removed sequentially using a backward selection procedure.

i.e. > 500 individuals) and hunting activity (Table 1; Fig. 2). Lapwings were more likely to fly on hunting days than on days before hunting ($F_{1,233} = 33.09$; $P < 0.001$) or after hunting ($F_{1,250} = 6.73$; $P = 0.009$), and also on days after hunting than on days before hunting ($F_{1,250} = 14.61$; $P = 0.001$).

For golden plovers, variation in flight probability was not significantly explained by sampling date or flock size, but was explained by daytime period (birds were more likely to fly AM than PM) and hunting activity (Table 1; Fig. 2). Golden plovers were more likely to fly on hunting days than on days before hunting ($F_{1,92} = 9.46$; $P = 0.002$), and on days after hunting than on days before hunting ($F_{1,130} = 12.16$; $P < 0.001$), but not on days after hunting as compared with hunting days ($F_{1,113} = 0.47$; $P = 0.495$).

Time spent vigilant

Variation in the % time spent vigilant by little bustards was explained by daytime period (birds spent more time vigilant AM than PM), sampling date (vigilance increased non-linearly, peaking at the end of the study period), flock size (vigilance tended to decrease linearly with increasing group size) and by hunting activity (Table 1; Fig. 2). Little bustards spent more time vigilant on hunting days than on days before hunting ($F_{1,169} = 16.77$; $P < 0.001$) or after hunting ($F_{1,203} = 29.85$; $P < 0.001$). Time spent vigilant did not differ significantly between days before or after hunting ($F_{1,190} = 0.27$; $P = 0.607$).

For lapwings, variation in the % time spent vigilant by lapwings was explained by daytime period (birds spent more time vigilant PM than AM), sampling date (time spent vigilant increased linearly with date), flock size (vigilance decrease linearly with increasing group size) and by hunting activity (Table 1; Fig. 2). Lapwings spent more time vigilant on hunting days than on days before hunting ($F_{1,172} = 16.37$; $P < 0.001$) or after hunting ($F_{1,166} = 14.12$; $P < 0.001$), but time spent vigilant did not differ significantly between days before or after hunting ($F_{1,191} = 2.86$; $P = 0.087$).

For golden plovers, variation in the % time spent vigilant was only explained by hunting activity (Table 1; Fig. 2). Golden plovers spent more time vigilant on hunting days than on days before hunting ($F_{1,67} = 19.87$; $P < 0.001$) or after hunting ($F_{1,66} = 4.25$; $P = 0.043$), and also on days after hunting than on days before hunting ($F_{1,87} = 8.87$; $P = 0.004$).

Time spent resting

Variation in the % time spent resting by little bustards was significantly explained by flock size (quadratic relationship: resting increased with increasing group size, but decreased for largest groups) and by hunting activity (Table 1; Fig. 2), but not by daytime period or sampling date. Little bustards spent less time resting during a hunting day than on a day before hunting ($F_{1,169} = 10.55$; $P = 0.001$) or after hunting ($F_{1,203} = 16.74$; $P < 0.001$), but spent a similar amount of

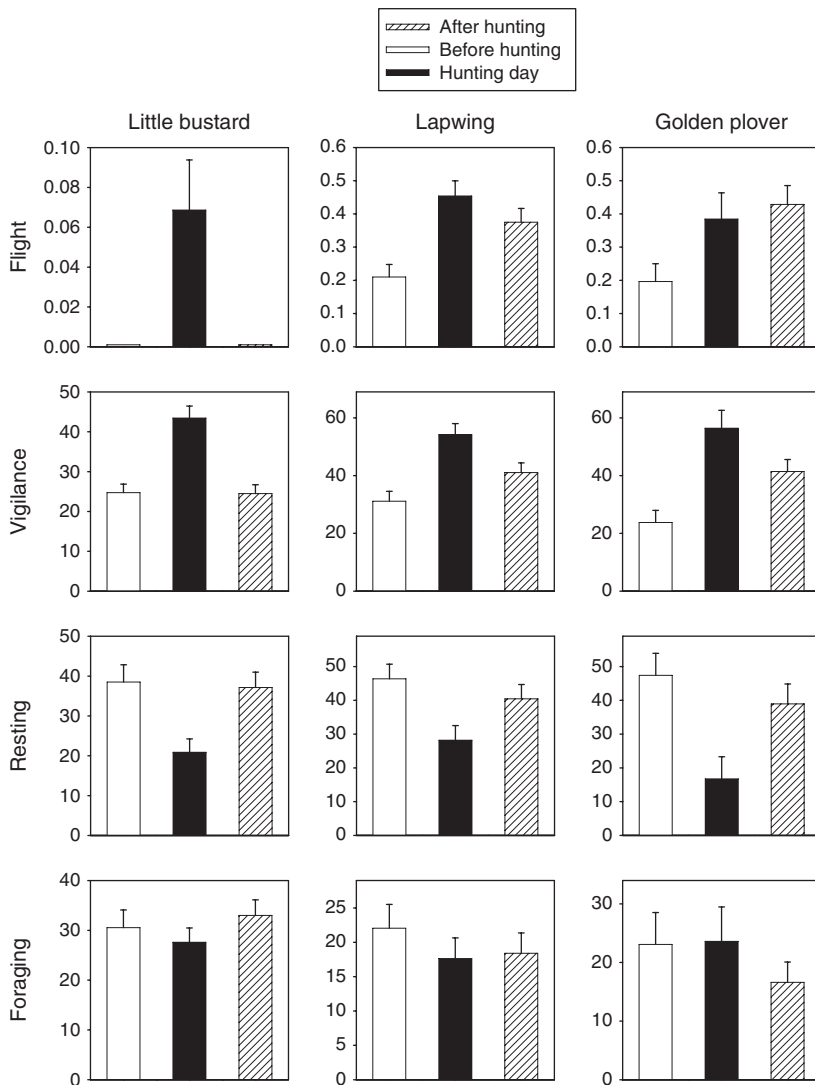


Figure 2 Mean \pm SE flight probability (top row), time spent vigilant (second row), time spent resting (third row) and time spent foraging (bottom row) by little bustards *Tetrax tetrax*, lapwings *Vanellus vanellus* and golden plover *Pluvialis apricaria* according to hunting activity (before a hunting day, when hunting took place and after a hunting day).

time resting on days before and after hunting ($F_{1,190} = 0.08$; $P = 0.772$).

For lapwings, variation in the % time spent resting was significantly explained by flock size (resting increasing linearly with increasing group size) and by hunting activity (Table 1; Fig. 2), but not by daytime period or sampling date. Lapwings spent less time resting during a hunting day than on a day before hunting ($F_{1,174} = 6.98$; $P = 0.009$) or after hunting ($F_{1,168} = 5.22$; $P = 0.024$), but spent a similar amount of time resting on days before and after hunting ($F_{1,193} = 0.22$; $P = 0.643$).

For golden plovers, variation in the % time spent resting was only explained by hunting activity (Table 1; Fig. 2). Golden plovers spent less time resting during a hunting day than on a day before hunting ($F_{1,67} = 9.11$; $P = 0.004$) or after hunting ($F_{1,66} = 55.65$; $P = 0.020$), but spent a similar amount of time resting on days before and after hunting ($F_{1,87} = 0.92$; $P = 0.339$).

Time spent foraging

Variation in the time spent foraging by little bustards was only significantly explained by flock size (quadratic function; time spent foraging increased with increasing group size, but decreased in largest groups; Table 1).

For lapwings, variation in the time spent foraging was explained by daytime period (lapwing spent more time foraging AM than PM) and sampling date (time spent foraging decreased with date), but not by flock size or hunting activity (Table 1; Fig. 2).

For golden plovers, variation in the time spent foraging was not significantly explained by any of the studied variables (Table 1; Fig. 2).

Hunting and use of hunting-free reserves

We found significant differences in the use of hunting reserves before, during and after a hunting day by lapwing

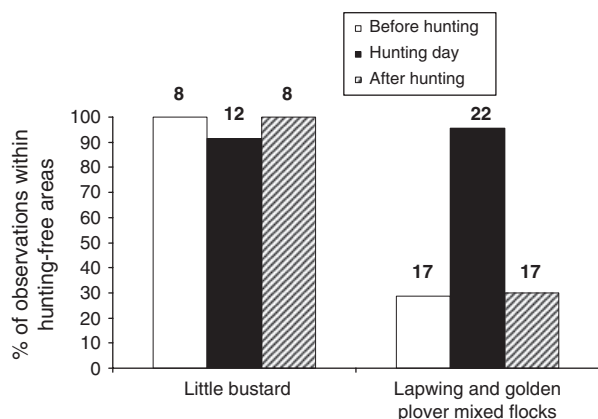


Figure 3 Use of hunting-free reserves (% of observations) by little bustards *Tetrax tetrax* flocks (left) and by mixed flocks of lapwings *Vanellus vanellus* and golden plovers *Pluvialis apricaria* (right) according to hunting activity: before a hunting day (white bars), during a hunting day (black bars) and after a hunting day (stripped bars). Sample size above bars refers to the total number of flocks observed during the study period.

and golden plover mixed flocks ($\chi^2 = 23\,581$; d.f. = 2, $P < 0.001$). Flocks were more often found within hunting reserves when hunting took place than when it did not (Wald = 12 234; $P = 0.0022$; Fig. 3). Variation in the probability of using the reserve was not explained by flock size (Wald = 0.053; $P = 0.81$), daytime period (Wald = 0.17; $P = 0.67$), sampling date (Wald = 0.846; $P = 0.35$) or habitat (Wald = 2476; $P = 0.47$), nor by any of the interactions between these variables.

Little bustards almost exclusively used the hunting-free area. All but one of the observations of little bustards ($n = 26$) were inside the hunting reserve (Fig. 3).

Discussion

We found that all three studied species showed behavioural as well as distributional responses to hunting activities, after considering other possible sources of variations, such as flock size, time of day or date. The effects of the latter depended on the species (see supporting information for a detailed discussion about this), while the effect of hunting disturbance was fairly consistent across species. Thus, hunting activities caused disturbance (changes in behaviour), and birds were more often disturbed during hunting days, avoided areas with hunting and used more often hunting-free areas. Because we found similar behavioural effects of hunting activity on northern lapwings, golden plovers and little bustards, hunting might similarly affect other birds within the community. Hunting disturbance caused increased flight frequency and time spent vigilant to the detriment of resting, which implies greater energetic costs, and may result in reduced condition or a greater predation risk (West *et al.*, 2002; B  chet, Giroux & Gauthier, 2004; Jarvis, 2005). However, we found no evidence that it affected the time spent feeding or foraging. These beha-

vioural effects were consistently found in the three studied species, and similar to those found in other species (Ridington *et al.*, 1996; Madsen, 1998a,b; F  ret *et al.*, 2003). Lapwings and golden plovers also spent more time flying after a hunting day, indicating that the disturbance effects may last at least for a day after the hunting activity had ceased. This effect might be the sum of a behavioural and distributional change caused by hunting disturbance, since birds used hunting-free reserves mainly on hunting days and the area around reserve on other days. Little bustards and lapwings resumed quickly to a normal vigilance rate after a hunting day. However, golden plovers remained more vigilant after a hunting day, suggesting that they might be less tolerant and particularly sensitive to this type of disturbance.

In order to save energy, birds usually resort to resting. In migratory species, like the study species, fat storage is particularly important before the migration (Berthold, 2002; F  ret *et al.*, 2003). Hunting disturbance might reduce nutrient storage by increasing time spent flying or vigilant (F  ret *et al.*, 2003; B  chet *et al.*, 2004). We did not find that time spent foraging decreased with hunting activity, but flight probability increased on hunting days, which implies a greater energy expenditure. The time spent foraging by lapwings and golden plovers were lower than for little bustard, may be because they are more nocturnal feeders than little bustards and could therefore complement their food (Gillings, Fuller & Sutherland, 2005).

Hunting activity and use of hunting-free reserves

Little bustards almost never left the hunting reserves during hunting season, and may be thus particularly sensitive to this type of disturbance. Hunting-free reserves appeared crucial for this endangered species. In contrast, lapwings and golden plovers used the hunting reserves mostly when hunting activity took place, but quickly resumed using other areas as soon as hunting stopped. Therefore, a game management plan based on reducing the number of hunting days per week (like the one implemented in many rural areas in France) could be enough to minimize the impact of hunting disturbance on some species, but not in others. Madsen (1998b) did not find a preferential use of hunting-free reserves by lapwings and golden plovers, but his study focused on migratory waterfowl, and was thus designed to study primarily the usefulness of hunting reserves in wetlands for waterbirds (protected areas had limited shore and did not include adjacent terrestrial habitats, which may be more important for wintering lapwings and plovers than shores). In fact, when including adjacent terrestrial habitats into the hunting-free reserves for waterfowl, golden plovers and lapwings moved to non-hunted areas as a quick response to the start of hunting activity (Bregnballe & Madsen, 2004).

Our findings are consistent with previous works conducted mainly on wetland and forest game species (e.g. Ebbinge, 1991; Percival, Halpin & Houston, 1997; B  chet

et al., 2004; Bregnballe & Madsen, 2004; Duriez *et al.*, 2005). They highlight that hunting-free reserves play a crucial role for the management of game species as well as for the conservation of threatened ones, like little bustards in our study. Furthermore, if reserves are hunting-free all year round, they should also benefit breeding birds when hunting also occurs during breeding season.

Management implications

With the necessary caution when dealing with results obtained at a local level, our findings showed similar disturbance effects of hunting activity on three species that share the same habitat (agricultural area) at the beginning of the hunting season. These three species had different life histories and ecological requirements, suggesting that hunting disturbance may affect a wide range of species. Hunting caused behavioural changes and displacement of birds from hunting areas to reserves areas on hunting days. Hunting-free reserves can thus mitigate the effect of hunting activities and help species of conservation concern in agricultural areas.

However, at least three caveats to that efficacy could be raised. First, some species particularly sensitive to hunting disturbance could restrict themselves to game reserves during hunting season. This was apparent for little bustards in our study. Species confined within hunting-free reserves might have a reduced choice of feeding habitats. For little bustards, crops such as rape-seed or alfalfa, are particularly important for foraging at this time of year (pers. obs.; Wolff *et al.*, 2001), probably because they provide relatively high energy as compared with other available crops. Therefore, habitat availability inside and outside the hunting reserves should be an important factor to consider in the design of these reserves in areas within the range of this endangered species.

Second, we detected some differences in the level of sensitivity to hunting disturbance, from complete confinement to hunting-free areas in the case of little bustards, to movements in and out of reserves depending on hunting activities in the case of golden plovers and lapwings. Studies on the effects of hunting disturbance should be conducted on a wide range of species to better understand the real impact of hunting disturbance on the whole community (Gill, Norris & Sutherland, 2001). Because numerous, repeated small disturbances could be more damaging than fewer, large disturbances (West *et al.*, 2002), the frequency of hunting activity could be regulated to reduce its impact on birds. A useful tool could be the use of behaviour-based individual model to quantify the potential impacts of hunting disturbance on individual survival and long-term population size (West *et al.*, 2002; Goss-Custard *et al.*, 2006; Stillman *et al.*, 2007), especially in the case of threatened farmland birds. Such models could help evaluate the best ways to minimize the impact of hunting disturbance.

Finally, birds might habituate to local levels of disturbance, becoming more tolerant in more disturbed areas (Blumstein *et al.*, 2005), which could make them more

susceptible to predation (Webb & Blumstein, 2005). Game reserves considered in this study were recently created (1991), and it could be useful to replicate this kind of study in areas where reserves have been established for longer periods.

An increase in the size of hunting-free areas might mitigate hunting disturbance, and could be an important management tool. This could be particularly important in areas where threatened species like little bustard are present, due their dramatic population declines in recent years (Morales *et al.*, 2005; Jolivet *et al.*, 2007). In such cases, another alternative might be the payment of incentives to hunters for increasing the size of the hunting-free areas. In any case, if an increase of hunting-free areas is applied as a hunting disturbance buffer, it is important to identify minimum size and threshold levels of disturbance that can be compatible for hunting activity and conservation.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix. Additional methods and discussion regarding the influence of factors other than hunting on the behaviour of study species.

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