

Full title: Effects of hunting on the behaviour and spatial distribution of farmland birds:
Importance of hunting-free refuges in agricultural areas.

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Short title: Hunting effects on behaviour and reserve use.

SUMMARY

Hunting is one of human activities that affect directly 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.

Keywords: disturbance, hunting, *Pluvialis apricaria*, reserves, *Tetrax tetrax*, *Vanellus vanellus*.

1 INTRODUCTION

2
3 Animals can perceive humans as potential predators and often alter their behaviour in
4 the presence of people. The increase in human population and leisure activities has
5 amplified the potential consequences of human disturbances on wildlife (Blanc *et al.*,
6 2006), including wild birds (Stockwell, Bateman & Berger, 1991; Madsen & Fox, 1995;
7 Fox & Madsen, 1997; Bautista *et al.*, 2005; Arroyo & Razin, 2006). However, the
8 overall effects of increasing human disturbance on bird populations are still poorly
9 documented (Guillemain *et al.*, 2007), and there is often much debate about how human
10 activities should be regulated (see e.g. González *et al.*, 2007 and references therein).

11 Hunting is one of the human activities that affect wildlife most, and it has
12 received increasing attention given its environmental, social and economic dimensions,
13 particularly in Europe (Lucio & Purroy, 1992; Martínez, Viñuela & Villafuerte, 2002).
14 However, hunting activity can be compatible with a conservationist policy, promoting
15 and financing preservation of natural ecosystems, in a context of “wise use”, whenever
16 an adequate management plan is implemented, adjusting human traditional activities,
17 hunting and wildlife conservation (Lucio & Purroy, 1992; Tapper, 1999; Robinson &
18 Bennett, 2004).

19 Most studies on the effect of hunting disturbance on birds have been conducted
20 on coastal, wetland and forest birds, mainly focusing on game species (Madsen & Fox,
21 1995; Fox & Madsen, 1997; Bregnballe, Madsen, & Rasmussen, 2004; Duriez *et al.*,
22 2005; Klaassen *et al.*, 2006; Stafford *et al.*, 2007; Thiel *et al.*, 2007; Thiollay, 2007).
23 These studies have evidenced that hunting causes local disturbance effects on target
24 game species, and may also affect other species of conservation concern (Madsen &
25 Fox, 1995; Fox & Madsen, 1997; Madsen, 1998*b*). Nevertheless, the effects that

1 hunting and game management have on non-target protected species are still poorly
2 known (Arroyo & Beja, 2002). In a recent attempt to reduce the impact of hunting on
3 wildlife, hunting reserves, where birds can benefit from reduced disturbance have been
4 created in North America and in several European countries (e.g. Madsen, 1998a, b;
5 Stafford *et al.*, 2007), but their efficiency as management tools has been poorly
6 investigated yet (Duriez *et al.*, 2005). Refuge size, location and network structure must
7 ensure birds find all their biological requirements, reducing to a minimum the external
8 disturbance (Fox & Madsen, 1997).

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

23 Our aim here is to evaluate the effect of hunting activities on the behaviour and
24 the use of hunting-free areas of birds that inhabit agricultural areas in Western France.
25 We focused on behaviours such as time spent flying, or vigilant to the detriment of

1 feeding or resting, which might indicate indirect costs of hunting activities to farmland
2 birds. We selected the northern lapwing (*Vanellus vanellus*; hereafter “lapwing”), the
3 european golden plover (*Pluvialis apricaria*; hereafter “golden plover”) and the little
4 bustard (*Tetrax tetrax*) as model species. Golden plover and lapwing are classified as
5 “not globally threatened” (del Hoyo, Elliot & Sargatal 1996) and are hunted in France.
6 In contrast, the little bustard is fully protected since 1972; it is currently classified as
7 “Vulnerable” in Europe (Goriup, 1994) and “red-listed” in France (Rocamora &
8 Yeatman-Berthelot, 1999). Farmland habitats in western France hold c.80 % of the
9 country’s population of little bustards (Jolivet *et al.*, 2007), which has suffered dramatic
10 declines in recent years (Morales, Bretagnolle & Arroyo, 2005; Jolivet *et al.*, 2007). In
11 autumn, when the study was conducted, little bustards prepare for their southward
12 migration (to Spain), while lapwings and golden plovers arrive for wintering on the
13 study area.

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

21 22 **MATERIAL AND METHODS**

23 24 **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 (2nd October – 6th December). This year, hunting season legally opened 5th 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 3-6 hunters, spaced every c. 40-50 metres. Within the study area, hunting is permitted in some areas, but not in other, which 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) 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 sec (± 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 minutes before starting another focal sampling on another individual. Birds were not individually marked, but we selected another bird that was at least at 10 metres 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 (Barnard, Thompson & Stephens, 1982; Cramp & Simmons, 1980, 1983; see also Electronic Supplementary Material 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 the followings: 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, 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 chi-square 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, ie. > 500 individuals) and hunting activity (Table 1; Fig. 2). Lapwings were more likely to fly on hunting days than on days prior

to 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 prior to 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 prior to 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 prior to 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 prior to 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 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

1 hunting day than on a day before hunting ($F_{1,67} = 9.11$; $P = 0.004$) or after hunting ($F_{1,66}$
2 $= 55.65$; $P = 0.020$), but spent a similar amount of time resting on days before and after
3 hunting ($F_{1,87} = 0.92$; $P = 0.339$).

4 5 *Time spent foraging.*

6
7 Variation in the time spent foraging by little bustards was only significantly explained
8 by flock size (quadratic function; time spent foraging increased with increasing group
9 size, but decreased in largest groups; Table 1).

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

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

15 16 *Hunting and use of hunting-free reserves*

17
18 We found significant differences in the use of hunting reserves before, during and after
19 a hunting day by lapwing and golden plover mixed flocks ($\chi^2=23,581$; d.f.=2, $P< 0.001$).
20 Flocks were more often found within hunting reserves when hunting took place than
21 when it did not (Wald=12,234; $P=0,0022$; Fig. 3). Variation in the probability of using
22 the reserve was not explained by flock size (Wald=0,053; $P=0,81$), daytime period
23 (Wald=0,17; $P=0,67$), sampling date (Wald=0,846; $P=0,35$) or habitat (Wald=2,476;
24 $P=0,47$), nor by any of the interactions between these variables.

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

3 4 **DISCUSSION**

5
6 We found that all three studied species showed behavioural as well as distributional
7 responses to hunting activities, after considering other possible sources of variations,
8 such as flock size, time of day, or date. The effects of the latter depended on the species
9 (see ESM for a detailed discussion about this), while the effect of hunting disturbance
10 was fairly consistent across species. Thus, hunting activities caused disturbance
11 (changes in behaviour), and birds were more often disturbed during hunting days,
12 avoided areas with hunting and used more often hunting-free areas. Because we found
13 similar behavioural effects of hunting activity on northern lapwings, golden plovers and
14 little bustards, hunting might similarly affect other birds within the community. Hunting
15 disturbance caused increased flight frequency and time spent vigilant to the detriment of
16 resting, which implies greater energetic costs, and may result in reduced condition or a
17 greater predation risk (West *et al.*, 2002; Béchet *et al.*, 2004; Jarvis, 2005). However,
18 we found no evidence that it affected the time spent feeding or foraging. These
19 behavioural effects were consistently found in the three studied species, and similar to
20 those found in other species (Riddington *et al.*, 1996; Madsen 1998a, b; Féret *et al.*,
21 2003). Lapwings and golden plovers also spent more time flying after a hunting day,
22 indicating that the disturbance effects may last at least for a day after the hunting
23 activity had ceased. This effect might be the sum of a behavioural and distributional
24 change caused by hunting disturbance, since birds used hunting-free reserves mainly on
25 hunting days and the area around reserve on other days (see below). Little bustards and

1 lapwings resumed quickly to a normal vigilance rate after a hunting day. However,
2 golden plovers remained more vigilant after a hunting day, suggesting that they might
3 be less tolerant and particularly sensitive to this type of disturbance.

4 In order to save energy, birds usually resort to resting. In migratory species, like
5 the study species, fat storage is particularly important prior to the migration (Féret *et al.*,
6 2003; Berthold, 2002). Hunting disturbance might reduce nutrient storage by increasing
7 time spent flying or vigilant (Féret *et al.*, 2003; Béchet *et al.*, 2004). We did not find
8 that time spent foraging decreased with hunting activity, but flight probability increased
9 on hunting days, which implies a greater energy expenditure. The time spent foraging
10 by lapwings and golden plovers were lower than for little bustard, may be because they
11 are more nocturnal feeders than little bustards and could therefore complement their
12 food (Gillings, Fuller & Sutherland, 2005).

14 *Hunting activity and use of hunting-free reserves*

16 Little bustards almost never left the hunting reserves during hunting season, and may be
17 thus particularly sensitive to this type of disturbance. Hunting-free reserves appeared
18 crucial for this endangered species. In contrast, lapwings and golden plovers used the
19 hunting reserves mostly when hunting activity took place, but quickly resumed using
20 other areas as soon as hunting stopped. Therefore, a game management plan based on
21 reducing the number of hunting days per week (like the one implemented in many rural
22 areas in France) could be enough to minimize the impact of hunting disturbance on
23 some species, but not in others. Madsen (1998b) did not find a preferential use of
24 hunting-free reserves by lapwings and golden plovers, but his study focused on
25 migratory waterfowl, and was thus designed to study primarily the usefulness of hunting

1 reserves in wetlands for waterbirds (protected areas had limited shore and did not
2 include adjacent terrestrial habitats, which may be more important for wintering
3 lapwings and plovers than shores). In fact, when including adjacent terrestrial habitats
4 into the hunting-free reserves for waterfowl, golden plovers and lapwings moved to
5 non-hunted areas as a quick response to the start of hunting activity (Bregnballe &
6 Madsen, 2004).

7 Our findings are consistent with previous works conducted mainly on wetland
8 and forest game species (e.g, Ebbinge, 1991; Percival, Halpin & Houston, 1997; Béchet
9 *et al.*, 2004; Bregnballe & Madsen, 2004; Duriez *et al.*, 2005). They highlight that
10 hunting-free reserves play a crucial role for the management of game species as well as
11 for the conservation of threatened ones, like little bustards in our study. Furthermore, if
12 reserves are hunting-free all year round, they should also benefit breeding birds when
13 hunting also occurs during breeding season.

14 15 *Management implications*

16
17 With the necessary caution when dealing with results obtained at a local level, our
18 findings showed similar disturbance effects of hunting activity on three species that
19 share the same habitat (agricultural area) at the beginning of the hunting season. These
20 three species had different life histories and ecological requirements, suggesting that
21 hunting disturbance may affect a wide range of species. Hunting caused behavioural
22 changes and displacement of birds from hunting areas to reserves areas on hunting days.
23 Hunting-free reserves can thus mitigate the effect of hunting activities and help species
24 of conservation concern in agricultural areas.

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

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

24 Finally, birds might habituate to local levels of disturbance, becoming more
25 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 to be compatible for hunting activity and conservation.

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BIBLIOGRAPHY

Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* **15**, 225-267.

- 1 Arroyo, B. & Beja, P. (2002). *Impact of hunting management practices on biodiversity*.
2 Report WP2 to REGHAB project. ([http://www.uclm.es/irec/reghab/](http://www.uclm.es/irec/reghab/informes.htm)
3 informes.htm) European Commission, Brussels.
- 4 Arroyo, B. & Razin, M. (2006). Effect of human activities on bearded vulture behaviour
5 and breeding success in the French Pyrenees. *Biol. Conserv.* **128**, 276-284.
- 6 Barnard, C.J., Thompson, D.B.A. & Stephens, H. (1982). Time budgets, feeding
7 efficiency and flock dynamics in mixed species flocks of lapwings, golden
8 plovers and gulls. *Behaviour* **80**, 44-69.
- 9 Bautista, L.M., Garcia, J.T., Calamaestra, R.G., Palacin, C., Martin, C.A., Morales,
10 M.B., Bonal, R. & Viñuela, J. (2005). Effect of weekend road traffic on the use
11 of space by raptors. *Conserv. Biol.* **18**, 726-732.
- 12 Béchet, A., Giroux, J.F. & Gauthier, G. (2004). The effects of disturbance on behaviour,
13 habitat use and energy of spring staging snow geese. *J. Appl. Ecol.* **41**, 689-700.
- 14 Bernabeu, R.L. (2000). *Evaluación económica de la caza en Castilla-La Mancha*. PhD
15 Thesis, Universidad de Castilla-La Mancha, Spain.
- 16 Berthold, P. (2002). *Bird migration. A general survey*. 2nd edn. Oxford University
17 Press, Oxford.
- 18 Blanc, R., Guillemain, M., Mouronval, J.B., Desmonts, D. & Fritz, H. (2006). Effects of
19 non-consumptive leisure disturbance to wildlife. *Revue D Ecologie-la Terre et la*
20 *Vie* **61**, 117-133.
- 21 Blumstein, D.T., Fernandez-Juricic, E., Zollner, P.A. & Garity, S.C. (2005). Inter-
22 specific variation in avian responses to human disturbance. *J. Appl. Ecol.* **42**,
23 943-53.

- 1 Bregnballe, T. & Madsen, J. (2004). Tools in waterfowl reserve management: effects of
2 intermittent hunting adjacent to a shooting-free core area. *Wildl. Biol.* **10**, 261-
3 268.
- 4 Bregnballe, T., Madsen, J. & Rasmussen, P.A.F. (2004). Effects of temporal and spatial
5 hunting control in waterbirds reserves. *Biol. Conserv.* **119**, 93-104.
- 6 Cramp, S. & Simmons, K.E.L. (1980). *The Birds of the Western Palearctic: Hawks to*
7 *Bustards*. Vol. II. Oxford University Press, Oxford.
- 8 Cramp, S., Simmons, K.E.L., 1983. *The Birds of the Western Palearctic: Waders to*
9 *Gulls*. Vol. III: Oxford University Press, Oxford.
- 10 del Hoyo, J., Elliott, A. & Sargatal, J. 1996. *Handbook of the Birds of the World, Vol.*
11 *III. Hoatzin to Auks*. Lynx Edicions, Barcelona.
- 12 Donald, P.F., Green, R.E. & Heath, M.F. (2001). Agricultural intensification and the
13 collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* **268**, 25-
14 29.
- 15 Duriez, O., Eraud, C., Barbraud, C. & Ferrand, Y. (2005). Factors affecting population
16 dynamics of Eurasian woodcocks wintering in France: assessing the efficiency
17 of a hunting-free reserve. *Biol. Conserv.* **122**, 89-97.
- 18 Ebbinge, B.S. (1991). The impact of hunting on mortality rates and spatial distribution
19 of geese wintering in the western palearctic. *Ardea* **79**, 197-210.
- 20 Fox, A.D. & Madsen, J. (1997). Behavioural and distributional effects of hunting
21 disturbance on waterbirds in Europe: implications for refuge design. *J. Appl.*
22 *Ecol.* **34**, 1-13.
- 23 Féret, M., Gauthier, G., Bechet, A., Giroux, J.F., Hobson, K.A., 2003. Effect of a spring
24 hunt on nutrient storage by greater snow geese in southern Québec. *J. Wildl.*
25 *Mgmt.* **67**, 796-807.

- 1 Gill, J.A., Norris, K. & Sutherland, W.J. (2001). Why behavioural responses may not
2 reflect the population consequences of human disturbance. *Biol. Conserv.* **97**,
3 265-268.
- 4 Gillings, S., Fuller, R.J. & Sutherland, W.J. (2005). Diurnal studies do not predict
5 nocturnal habitat choice and site selection of European Golden-Plovers
6 (*Pluvialis apricaria*) and Northern Lapwings (*Vanellus vanellus*). *The Auk* **122**,
7 1249-1260.
- 8 González, L.M., Arroyo, B.E., Margalida, A., Sánchez, R. & Oria, J. (2007). Can buffer
9 zones have detrimental effects on the conservation of Spanish imperial eagles?:
10 a response from González et al. *Anim. Conserv.* **10**, 295-296.
- 11 Goriup, P. (1994). Little Bustard *Tetrax tetrax*. In *Birds in Europe: Their Conservation*
12 *Status*: 236-237. Tucker, G.M. & Heath, M.F. (Eds.) Birdlife International,
13 Cambridge.
- 14 Goss-Custard, J.D., Triplet, P., Sueur, F. & West, A.D. (2006). Critical thresholds of
15 disturbance by people and raptors in foraging wading birds. *Biol. Conserv.* **127**,
16 88-97.
- 17 Guillemain, M., Blanc, R., Lucas, C. & Lepley, M. (2007). Ecotourism disturbance to
18 wildfowl in protected areas: historical, empirical and experimental approaches in
19 the Camargue, Southern France. *Biodivers. Conserv.* **16**, 3633-3651.
- 20 Howard, N. & Carroll, J. (2001). Driven game shooting on farms in Essex, UK:
21 Implications of land management and conservation. *Game Wildl. Science* **18**,
22 157-169.
- 23 Jarvis, P.J. (2005). Reaction of animals to human disturbance, with particular reference
24 to flight initiation distance. *Recent Res. Develop. Ecol.* **3**, 1-20.

- 1 Jolivet, C., Bretagnolle, V., Bizet, D. & Wolff, A. (2007). Status of little bustard in
2 France in 2004. *Ornithos* **14**, 80-94.
- 3 Klaassen, M., Bauer, S., Madsen, J. & Ingunn, T. (2006). Modelling behavioural and
4 fitness consequences of disturbance for geese along their spring flyway. *J. Appl.*
5 *Ecol.* **43**, 92-100.
- 6 Lucio, A.J. & Purroy, F.J. (1992). Caza y conservación en España. *Ardeola* **39**, 85-98.
- 7 Madsen, J. & Fox, A.D. (1995). Impacts of hunting disturbance on waterbirds-A review.
8 *Wildl. Biol.* **1**, 193-207.
- 9 Madsen, J. (1998a). Experimental refuges for migratory waterfowl in Danish wetlands.
10 I. Baseline assessment of the disturbance effects of recreational activities. *J.*
11 *Appl. Ecol.* **35**, 386-397.
- 12 Madsen, J. (1998b). Experimental refuges for migratory waterfowl in Danish wetlands.
13 II. Tests of hunting disturbance effects. *J. Appl. Ecol.* **35**, 398-417.
- 14 Martínez, J., Viñuela, J. & Villafuerte, R. (2002). *Socioeconomic and cultural aspects*
15 *of gamebird hunting*. REGHAB project, European Commission, Brussels,
16 Belgium.
- 17 Morales, M.B., Bretagnolle, V. & Arroyo, B. (2005). Viability of the endangered little
18 bustard *Tetrax tetrax* population of western France. *Biodivers. Conserv.* **14**,
19 3135-3150.
- 20 Percival, S.M., Halpin, Y. & Houston, D.C. (1997). Managing the distribution of
21 barnacle geese on Islay, Scotland, through deliberate human disturbance. *Biol.*
22 *Conserv.* **82**, 273-277.
- 23 Riddington, R., Hassall, M., Lane, S.J., Turner, P.A. & Walters, R. (1996). The impact
24 of disturbance on the behaviour and energy budgets of Brent geese *Branta b.*
25 *bernicla*. *Bird Study* **43**, 269-279.

- 1 Robinson, R.A. & Sutherland, W.J. (2002). Post-war changes in arable farming and
2 biodiversity in Great Britain. *J. Appl. Ecol.* **39**, 157-176.
- 3 Robinson, J.G. & Bennett, E.L. (2004). Having your wildlife and eating it too: an
4 analysis of hunting sustainability across tropical ecosystems. *Anim. Conserv.* **7**,
5 397-408.
- 6 Rocamora, G. & Yeatman-Berthelot, D. (1999). *Oiseaux menacés et à surveiller en*
7 *France: listes rouges et recherche de priorités*. Société d'Études
8 Ornithologiques de France/Ligue pour la Protection des Oiseaux, Paris.
- 9 Roth, T.C. & Lima, S.L. (2007). The predatory behavior of wintering *Accipiter* hawks:
10 temporal patterns in activity of predators and prey. *Oecologia* **152**, 169-178.
- 11 Stafford, J.D., Horath, M.M., Yetter, A.P., Hine, C.S. & Havera, S.P. (2007). Wetland
12 use by mallards during spring and fall in the Illinois and Central Mississippi
13 River Valleys. *Waterbirds* **30**, 394-402.
- 14 Stillman, R.A., West, A.D., Caldow, R.W.G. & Durell, S.E.A.L.V.D. (2007). Predicting
15 the effect of disturbance on coastal birds. *Ibis* **149**, 73-81.
- 16 Stockwell, C.A., Bateman, G.C. & Berger, J. (1991). Conflicts in national parks: a case
17 study of helicopters and bighorn sheep time budgets at the Grand Canyon. *Biol.*
18 *Conserv.* **56**, 317-328.
- 19 Tapper, S. (1999). *A Question of Balance*. The Game Conservancy Trust,
20 Fordingbridge, Hampshire.
- 21 Thiel, D., Ménoni, E., Brenot, J.F. & Jenni, L. (2007). Effects of recreation and hunting
22 on flushing distance of Capercaillie. *J. Wildl. Mgmt.* **71**, 1784-1792.
- 23 Thiollay, J.M. (2007). Effects of hunting on guianan forest game birds. *Biodivers.*
24 *Conserv.* **14**, 1121-1135.

- 1 Tucker, G.M. & Heath, M.F. (1994). *Birds in Europe: their conservation status*.
2 Birdlife International, Cambridge.
- 3 Webb, N.V. & Blumstein, D.T. (2005). Variation in human disturbance differentially
4 affects predation risk assessment in Western Gulls. *Condor* **107**, 178-181.
- 5 West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W.G., Durell, S.E.A.l.V.d.
6 & McGrorty, S. (2002). Predicting the impacts of disturbance on shorebird
7 mortality using a behaviour-based model. *Biol. Conserv.* **106**, 319-328.
- 8 Wolff, A., Paul, J.P., Martin, J.L. & Bretagnolle, V. (2001). The benefits of extensive
9 agriculture to birds: the case of the little bustard. *J. Appl. Ecol.* **38**, 963-975.

10

1 Table 1. Effects of daytime period, date, group size and hunting activity on the behaviour of studied species. Only the final models are presented.
2 All initial models included daytime period (am vs pm), sampling date and sampling date², group size and group size² (to test for linear or
3 quadratic relationships with date or group size) and hunting activity (day before, during or after hunting took place). Non-significant variables (P
4 = 0.10 level) were removed sequentially using a backward selection procedure.

Behaviour	Source of variation	Little Bustard			Lapwing			Golden Plover		
		df	Chi ²	P	df	Chi ²	P	df	Chi ²	P
Flying probability	Daytime period	1,290	9.57	0.039	1,367	4.22	0.039	1,166	11.32	<0.001
	Flock size				1,367	6.08	0.014			
	Flock size ²				1,367	16.72	<0.001			
	Hunting activity	2,290	6.15	<0.001	2,367	34.53	<0.001	2,156	15.46	<0.001
		df	F	P	df	F	P	df	F	P
Vigilance	Daytime period	1,283	5.53	0.019	1,266	5.04	0.026			
	Date	1,283	6.70	0.010	1,266	4.11	0.044			
	Date ²	1,283	6.91	0.009						
	Flock size	1,283	3.49	0.063	1,266	4.93	0.027			
	Hunting activity	2,283	19.54	<0.001	2,266	9.93	<0.001	2,107	9.26	<0.001
Resting	Daytime period									
	Flock size	1,283	4.57	0.033	1,266	6.66	0.010			
	Flock size ²	1,283	6.34	0.012						
	Hunting activity	2,283	8.45	<0.001	1,266	3.19	0.043	2,107	6.57	0.002
Foraging	Daytime period				1,266	5.04	0.026			
	Date				1,266	7.70	0.006			
	Flock size	1,283	15.37	<0.001						
	Flock size ²	1,283	16.96	<0.001						
	Hunting activity	2,283	0.37	0.693	1,266	1.24	0.290	2,107	0.38	0.684

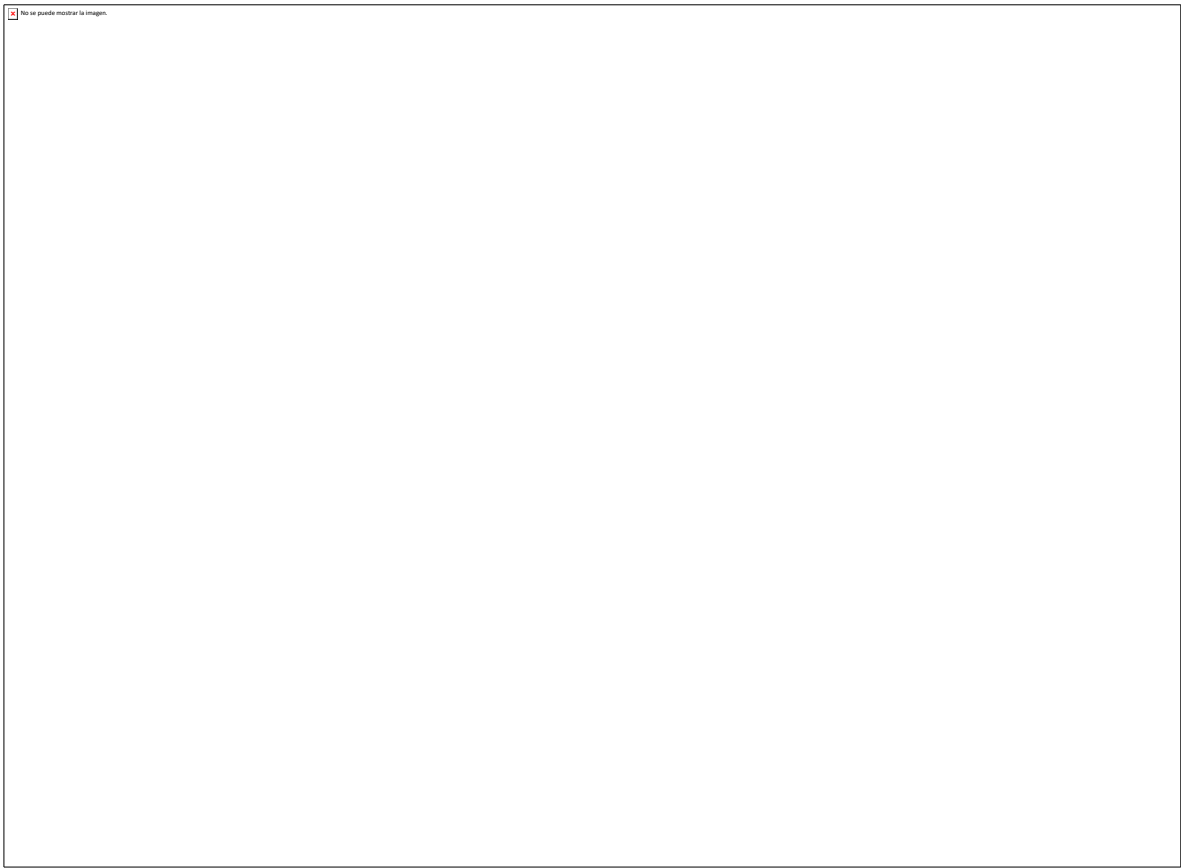
Figure legends:

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 methods). The dots show the locations of lapwing and golden plover mixed flocks during non-hunting days (black dots ●) and during hunting days (white dots ○).

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, lapwings and golden plover according to hunting activity (before a hunting day, when hunting took place and after a hunting day).

Figure 3. Use of hunting-free reserves (% of observations) by little bustards flocks (left) and by mixed flocks of lapwings and golden plovers (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.

1 Fig. 1



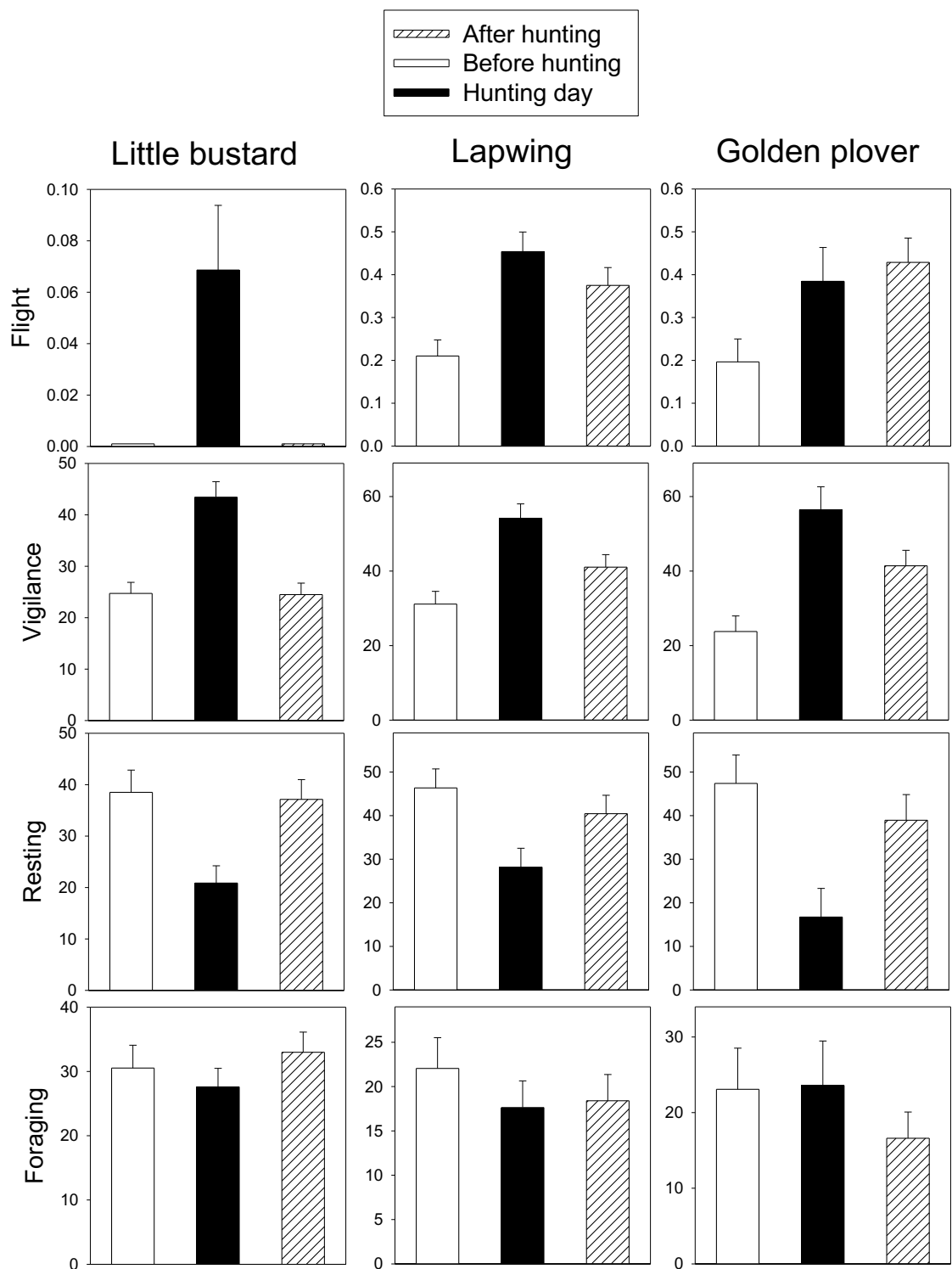
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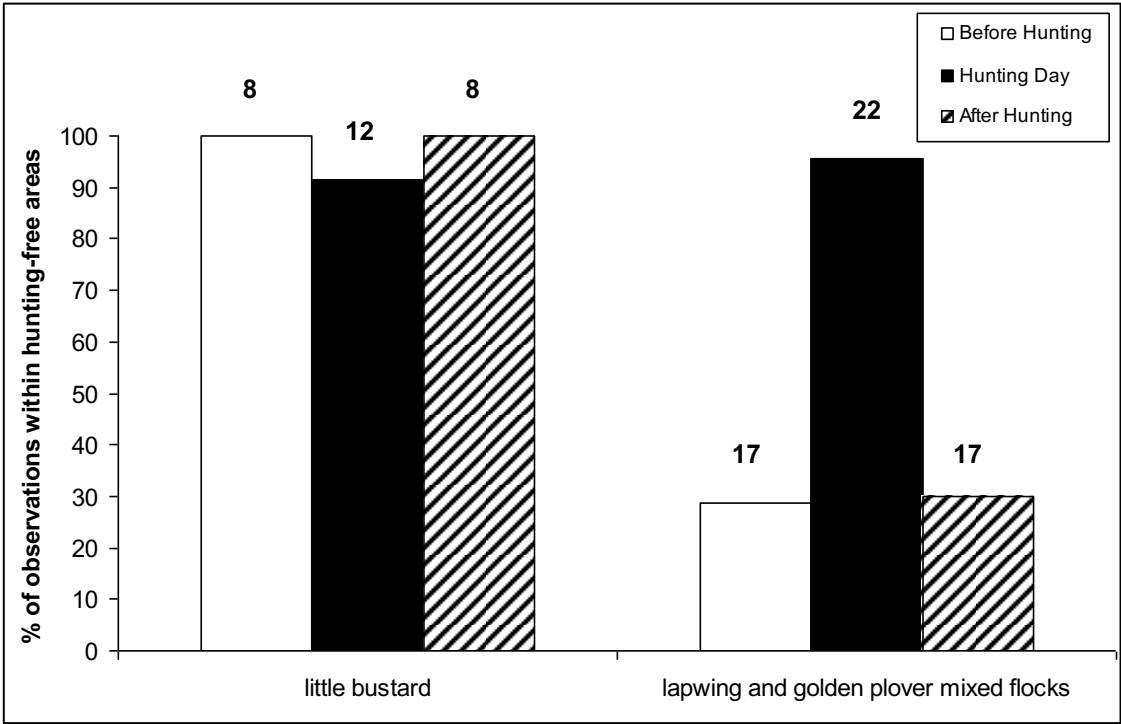
1 Fig. 2



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1 Fig. 3



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