manifesté un comportement territorial. Leurs domaines vitaux se chevau-
chaient à 82 % et ils étaient ensemble (à moins de 25 m l'un de l'autre) dans
83 % des localisations effectuées au cours de la période pré-incubatoire (du
2 avril au 4 mai). Il semble donc que le lien qui unit les membres d'un couple
soit fort et stable. Les deux mâles non-appariés ont présenté des comporte-
ments différents en avril. L'un a occupé un petit territoire de 2,1 ha (n = 31),
alors que l'autre avait un grand domaine vital de 31,3 ha (n = 33), apparem-
ment non-défendu et qui recouvrait en partie plusieurs territoires d'autres
mâles. Au début du mois de mai, les mâles appariés ont gardé les mêmes ter-
ritoires qu'en avril, alors que les mâles non-appariés se sont éloignés de 300
à 400 m des domaines vitaux qu'ils occupaient en avril. Nos données ne provien-
nent que de quelques gélinottes équipées d'émetteurs. Cependant, elles sug-
gèrent que, dans les montagnes de Changbai, les mâles appariés sont terri-
toriaux et qu'ils font partie de couples apparemment aussi étroitement unis
qu'en Suède. Ce comportement des gélinottes chinoises est différent de celui
des gélinottes de la région extrême orientale russe plus proche de la Chine.
Dans cette région, au printemps, les gelinottes ont probablement des défi-
ciences nutritionnelles dues aux hivers rigoureux. Cependant, les deux mem-
bres de notre couple marqué ont été trouvés ensemble plus souvent que les
membres des couples suédois. En Suède, les couples les plus unis étaient
ceux qui étaient situés dans les habitats avec les taux de prédation les plus
élevés. La relation étroite que nous avons observée entre les membres de
notre couple pourrait donc être liée aussi aux habitats de vieilles forêts de
feuillus des montagnes de Changbai, relativement plus ouverts et donc propices
à la prédation.

Trad. par E. Taran

NESTING SUCCESS OF GREY PARTRIDGES (PERDIX PERDIX) ON AGRICULTURAL LAND IN NORTH-CENTRAL FRANCE: RELATION TO NESTING COVER AND PREDATOR ABUNDANCE

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ABSTRACT

We monitored 1,009 radiotagged wild female grey partridges, Perdix perdix,
from March to September on 10 contrasting study areas to identify and quantify
the causes of nest failure. We recorded the fate of 407 first clutches and 141
replacement clutches. Simultaneously, we estimated the abundance of red
foxes, Vulpes vulpes, and mustelids, Mustelidae, and recorded nesting habitat
characteristics. Success rate varied significantly across study areas from 31%
(n = 16) to 73% (n = 46) for first clutches (p = 0.013), but not for replacement
clutches (range : 0%, n = 6; 53%, n = 16). Cereals were the best nesting cover
for first clutches (66% success rate, n = 232), whereas replacement clutches in
cereals suffered from harvesting in July (29% success rate, n = 45).
Nevertheless, the variation in success rate of first clutches across study areas
was not correlated with the variation in the amount of cereals. The main cause
of failure of first clutches (n = 150 clutches failed for identified causes) was
predation (70%), followed by farming practices (22%). Replacement clutches
(n = 79 clutches failed for identified causes) suffered from predation (51%) and
farming practices (43%). Ground carnivores (red foxes, mustelids and domestic
cats) were responsible for 66% of identified incubating-female predation cases
(n = 76) and for 36% of identified egg-predation cases (n = 69). The predation
rate on first clutches was positively correlated with the abundance of mustelids
(p = 0.008) but not of red foxes. Predation rate was especially high (46%)
in linear landscape features (n = 46). The results justify the local control of some
mustelid species to alleviate clutch losses, together with appropriate field
margin management that could be included as a partridge conservation
measure in the French scheme "Contrat Territorial d'Exploitation" (application of
the new CAP directives).

I. INTRODUCTION

Many bird species are currently reported as endangered or declining in Europe (in HAGEMEIJER and BLAIR, 1997). Among them, many inhabit agricultural land (TUCKER, 1997), like the grey partridge, Perdix perdix, which is a representative example (e.g. BIRKAN and JACOB, 1988; POTTS and AEBISCHER, 1995). POTTS (1997) estimated that the number of pairs has declined by 80% in Europe since the 1930s. As a result, the grey partridge has been listed as a species with an unfavourable conservation status in Europe (AEBISCHER and KAVANAGH, 1997), and has become an important management concern. Within Europe, the French grey partridge population is of great importance in terms of both breeding numbers and densities. Numbers have been estimated at 900,000 individuals, ranking France first by number in western Europe (AEBISCHER and KAVANAGH, 1997). Densities may still average 30 pairs/km² on large areas (REITZ, 1997; BRO et al., 2000a), and even exceed 60 pairs/km² on some intensively managed private land (Fédérations départementales des chasseurs, unpublished data). These densities are higher than the values of 5-20 pairs commonly reported on study areas in the United Kingdom (e.g. POTTS and AEBISCHER, 1995; TAPPER et al., 1996), Germany (e.g. KAISER, 1998) and Poland (e.g. PANEK and KAMIENIARZ, 1998).

As an important game bird in Europe, the grey partridge has been much studied. Losses occur at different critical stages: breeding females, clutches and chicks (e.g. BIRKAN and JACOB, 1988). Ecological studies have mostly focused on the last stage of breeding, brood-rearing (e.g. GREEN, 1984; SOTHERTON and ROBERTSON, 1990; PANEK, 1997), because several demographic analyses have shown that chick survival rate had the greatest effect on population fluctuations (BLANK et al., 1967; PODOLER and ROGERS, 1975; POTTS, 1980) and determined population status (POTTS and AEBISCHER, 1995). Moreover, the shooting bag is positively correlated with chick survival rate (POTTS and AEBISCHER, 1991), so this factor is of key importance to shooting interests. However, a supplementary hypothesis has recently arisen. POTTS and AEBISCHER (1995) reported that the decline of partridge numbers observed in the Sussex study area since the late 1960s was correlated with a decrease in brood-production rate, reflecting an increased mortality of breeding females and a high predation rate on clutches. A similar concern about female survival during breeding had been voiced in France in the early 1990s (REITZ, 1990; REITZ and BERGER, 1995). To investigate this aspect, we conducted a large field study by radiotracking 1,009 wild breeding females in 1995-1997 on ten study areas in North-Central France. This survey confirmed that females could suffer high mortality rates during the breeding season (BRO et al., 2001). Simulation modelling supported the hypothesis that the decline in adult survival rate could explain the depletion of grey partridge in some regions of France (BRO et al., 2000b).

As part of this study, we investigated the determinants of grey partridge nesting success. Our objectives were to (1) identify the causes of nest failure, (2) quantify the relative importance of losses to agricultural farming or predation depending upon nesting cover, and (3) test whether the predation rate on clutches was correlated with the abundance of predators. These results will provide management guidelines to increase breeding success by improving nesting success.

II. MATERIAL AND METHODS

II.1. STUDY AREAS

We monitored grey partridge nests on ten study areas (ranging from 20 to 150 km²) in contrasting farming regions of North-Central France (see Figure 1 in BRO et al., 2000a). These areas were chosen to reflect farmland diversity: land use was traditional (mixed arable and livestock farms) in the study areas A (located in the administrative department "Nord"), B ("Pas-de-Calais"), C ("Somme"), D ("Seine maritime"), and H ("Sarthe"). Other study sites were situated in open farmland of intensive cereal production (E: "Marne", F and G: "Aube", I and J: "Loiret"). A detailed description of farmland characteristics is given in BRO et al. (2000a). No particular habitat management or environmentally friendly farming practices were applied in the study areas. Partridge density in spring ranged from 3 to 28 pairs/km² (BRO et al., 2000a,b). Weather conditions were those of a mild temperate climate. The topography was flat to gently undulating.

II.2. CLUTCH SURVEY

We radiotracked breeding females to find nests. We captured 1,009 wild grey partridge females from mid-March to early April 1995-1997, after breeding pairs had formed and settled (see POTTS, 1980; BIRKAN and JACOB, 1988). Birds were captured at night with a hand-held net and using a strong light. Females were radio-tagged with 10-g necklace radio-transmitters (BRO et al., 1999), and then monitored daily until September.

The radio-transmitters were equipped with either a mortality sensor or an activity sensor (see BRO et al., 1999). The former mechanism indicated that birds were alive and the latter that birds were moving. In this last case, when birds were alive and the signal was recorded several times during the day until it was necessary, the signal was recorded several times during the day until it was positive. Therefore, incubating females could not be confused with dead birds.

Clutches could be located when incubation began because, then, females left their clutches only once or twice a day to feed (see POTTS, 1980; BIRKAN and JACOB, 1988). To confirm that most clutches were actually found during incubation, we calculated the time between the date of detection of a clutch and its date of hatching for 197 successful clutches. We found that 86.8% of clutches were discovered within 25 days before hatching (i.e., during the incubation period, considered to last 25 days; POTTS, 1980), and about 10% within more than 27 days before hatching (i.e., during the laying period).

The reproductive history of each female was known through radiotracking. Thus, first and replacement clutches had been identified. However, a first clutch lost during laying or early incubation could have gone undetected. Indeed, some clutches reported as first clutches were thought to have hatched too late (after mid-July) to be actual first clutches. In these cases, we assumed that clutches that hatched, or were expected to hatch, after mid-July were replacement clutches unless they had more than 15 eggs. Conversely, clutches with less than 11 eggs hatched, or expected to hatch, before mid-July were assumed to be replacement clutches (see BIRKAN and JACOB, 1988). When clutch data were less precise, we classified them as "unidentified clutch type" and did not include them in the analyses (n = 7, Appendix).

We recorded 407 first clutches and 141 replacement clutches (Appendix). The death of many females within the first week after release (BRO et al., 1999)

or before incubation (BRO *et al.,* 2001), and radio failures (BRO *et al.,* 1999) mainly explained the discrepancy between the number of radio-tagged females and the number of clutches found. Clutches were mostly visited after females had ceased incubation (i.e., after hatching, desertion or clutch destruction) to minimize predation and desertion risks induced by the observer (see NICHOLS *et al.,* 1984). Clutch fate was determined according to clutch condition (within 24 hr after failure, through the daily monitoring of females). Hatching was recognized by small regular breaks in the egg-shells, often with one half of the shell within the other one (BIRKAN and JACOB, 1988). The finding of intact cold eggs whilst the female was known to be alive was interpreted as nest desertion. Clutch destruction was attributed to farming practices when eggs were found broken and compressed into the nest, and to predation when large empty fragments of shell were found scattered around the nest. Putative predators were identified by the species- or group-specific breaks and punctures in the egg-shells caused by the teeth or beaks of predators (BIRKAN and JACOB, 1988). These criteria did not allow to identify a predator species with the same accuracy and reliability. For instance the presence of isolated small holes was a positive criterion to identify mustelids, *Mustelidae,* whereas such precise criteria were not available for red foxes, *Vulpes vulpes,* and corvids, *Corvidae,* which were probably classified as "unidentified predators". Thus, it is likely that the influence of mustelids was overestimated.

We recorded the habitat characteristics of nest sites, in particular the type of nesting cover and the distance from nest to field margin. Nesting cover was classified into six habitat types: cereals (wheat, barley, oats, rye), other crops (maize, sunflowers, oilseed rape, sugar beet, peas, potatoes, linseed), fodder crops (ray-grass, lucerne, clover), meadows (i.e., pastures), set-aside (all different types pooled), and linear landscape features (i.e., hedgerow, bank, roadside, ditch).

II.3. PREDATOR ABUNDANCE

Red fox abundance (kilometric index of abundance) was estimated in late February by driving slowly by car at night and counting the number of individuals detected along a road transect (with a length of 0.6 km per km² of study area) by using a hand-held light (STAHL, 1990; STAHL and MIGOT, 1990). We estimated the index of abundance in late winter because this was the most suitable period in terms of visibility (STAHL, 1990).

Mustelid abundance (potentially including the stone marten, *Martes foina,* the polecat, *Putorius putorius,* the pine marten, *Martes martes,* the weasel, *Mustela nivalis* and the stoat, *Mustela erminea*) was estimated in August-September through the presence of faeces along 30 1-km transects covered on foot on each study area. To sample the whole study area homogeneously, we cross-ruled the map into 30 equal squares. Within each square, one 1-km linear feature was selected as a sample (i.e., a hedge, wood edge, field boundary, lane). The index of abundance used was the proportion of transects with faeces (hereafter "positive transects"). Data were analysed through a presence-absence variable rather than using the number of faeces found along a given transect because this latter variable does not reflect the abundance of animals but a special behaviour. Two surveys were performed 15 days apart to test for the repeatability of the

minimum value assuming that a transect was positive only when both surveys were positive. The final index used in the statistical analysis was the average value of the maximum and minimum.

II.4. STATISTICAL ANALYSES

Success rate of the clutches was defined as the proportion of successful clutches (i.e., clutches for which at least one egg hatched) in a given study area. We distinguished between predation rate on incubating females and predation rate on clutches because predators of eggs and partridges supposedly were different ones. The analysis of predation on incubating females is relevant to a study of clutch success because the death of females during incubation leads to failure of the clutch. The predation rate on clutches was defined as the proportion of clutches that failed because of predation (i.e. number of clutches failed by predation divided by the total number of clutches recorded). The definition of the predation rate on incubating females was similar. The predation rates (and more generally the failure rates) estimated with our data corresponded to minimum values because failures during laying or early incubation were likely to go undetected.

We excluded from analyses the clutches whose fate was unknown (missing values: $n = 12$ for first clutches, $n = 0$ for replacement clutches), and those that were deserted immediately after being visited by an observer because abandonment could directly be related to disturbance ($n = 12$ for first clutches, $n = 6$ for replacement clutches). To take the sample size of the category "unidentified cause of clutch failure" into account, we considered that the proportion of clutches that failed because of predation within this category was the same as the proportion computed with the cases of identified causes of failure (i.e., the "pro-rata rule"). This procedure assumed that non-identified causes of failure were not biased. Differences in sample size in the results are due to missing values for other variables such as nesting cover or distance to the field margin.

Because a relatively small number of first and replacement clutches were described per study area and per year (at least for some study areas, Appendix), we focused our analyses on spatial and not on temporal variations, and pooled all 1995–1997 data. Similarly, for sample-size reasons, we did not analyse the data by including both all six categories of the nesting cover variable and all ten sites of the study area variable, and their interaction, but used the following analysis procedure. We examined the variation in the causes of clutch failure across study areas first, to correlate spatial differences with environmental conditions such as habitat availability and predator abundance. Then, we examined the differences in the pattern of clutch fate across nesting cover (by pooling data across study areas) to further investigate the influence of habitat.

First and replacement clutch data are *a priori* not independent because replacement clutches are laid by females that have already produced a first clutch which failed. Comparing the fate of first and replacement clutches by using paired analyses was not possible since all first clutches were unsuccessful. Thus, there is some pseudoreplication in the data used for the tests of comparison between nesting attempts.

Differences in clutch fate across study areas and across nesting cover types were investigated by a log-linear model (McCULLAGH and NELDER, 1983) (proc CATMOD, likelihood ratio chi-square, empty cells were forcibly consid-

1983) to examine the relationship between 1) variability of the predation rate across study areas and the abundance of red foxes and mustelids, 2) variability of success rate and the amount of cereals (proc GENMOD, binomial distribution, logit-link function, controlling for overdispersion, weighted analyses to take account of the number of clutches recorded on each study area). We used a logistic analysis at an individual scale to test whether predation risk was higher for clutches laid near field boundaries. One-tailed tests were performed when testing relationships for which we investigated only one deviation of the difference (i.e., whether the predation rate increased with predator abundance, or whether it was higher near field margins) (SOKAL and ROLHF, 1981).

III. RESULTS

III.1. SPATIAL VARIATION IN CLUTCH SUCCESS RATE

Clutch success rate differed between first and replacement clutches ($\chi^2_1 = 13.15$, $p < 0.001$). Success rate of first clutches varied significantly across study areas ($\chi^2_9 = 20.87$, $p = 0.013$) between 31% (area H, $n = 16$) and 72% (area D, $n = 46$) (Appendix). Success rate of replacement clutches ranged from 0% (area F, $n = 6$) to 53% (area D, $n = 16$), but did not vary significantly across study areas ($\chi^2_9 = 10.46$, n.s.). This could result from the smaller sample size per study area.

III.2. CAUSES OF CLUTCH FAILURE

The **pattern of failure** (i.e., the categories "death of incubating females", "clutch destruction" and "clutch desertion") did not vary simultaneously across study areas and clutch type (i.e., first type and replacement type) (interaction "pattern of failure * study area * clutch type": $\chi^2_{18} = 22.69$, n.s.), but differed significantly both across study areas ($\chi^2_{18} = 36.44$, $p = 0.006$) and between clutch types ($\chi^2_2 = 9.35$, $p = 0.009$). Failed first clutches ($n = 181$) suffered from the death of incubating females (40%), clutch destruction (34%) and clutch desertion (26%) in roughly similar proportions (Figure 1, Appendix), whereas clutch destruction (51%) was the main type of failure for failed replacement clutches ($n = 89$), before clutch desertion (27%) and death of the incubating clutches ($n = 89$), before clutch desertion (27%) and death of incubating females (22%) (Figure 1). However, in given study areas, the death of incubating females could reach 69% (area F, $n = 13$ failed first clutches), the desertion of first clutches 53% (area A, $n = 15$ failed clutches) and clutch destruction 75% (area C, $n = 16$ failed first clutches) (Appendix).

The **causes of clutch failure** (i.e., the categories "predation" – on both incubating females and eggs –, "farming practices", "other causes" – such as weather conditions) differed significantly between nesting attempts ($\chi^2_2 = 9.14$, $p = 0.010$) and moderately across study areas ($\chi^2_{18} = 28.46$, $p = 0.055$), the interaction "cause of failure * study area * clutch type" being non significant ($\chi^2_{18} = 25.35$, n.s.). First clutches ($n = 150$ clutches failed from identified causes) experienced high predation rates on both incubating females and eggs (70%), whereas replacement clutches ($n = 79$ clutches failed from identified causes) suffered more equal-ly from predation (51%) and farming practices (43%) (Figures 1 and 2). However,

Pattern of clutch failure   **Causes of clutch failure**

Legend:
- Death of incubating females
- Clutch destruction
- Clutch desertion
- Predation
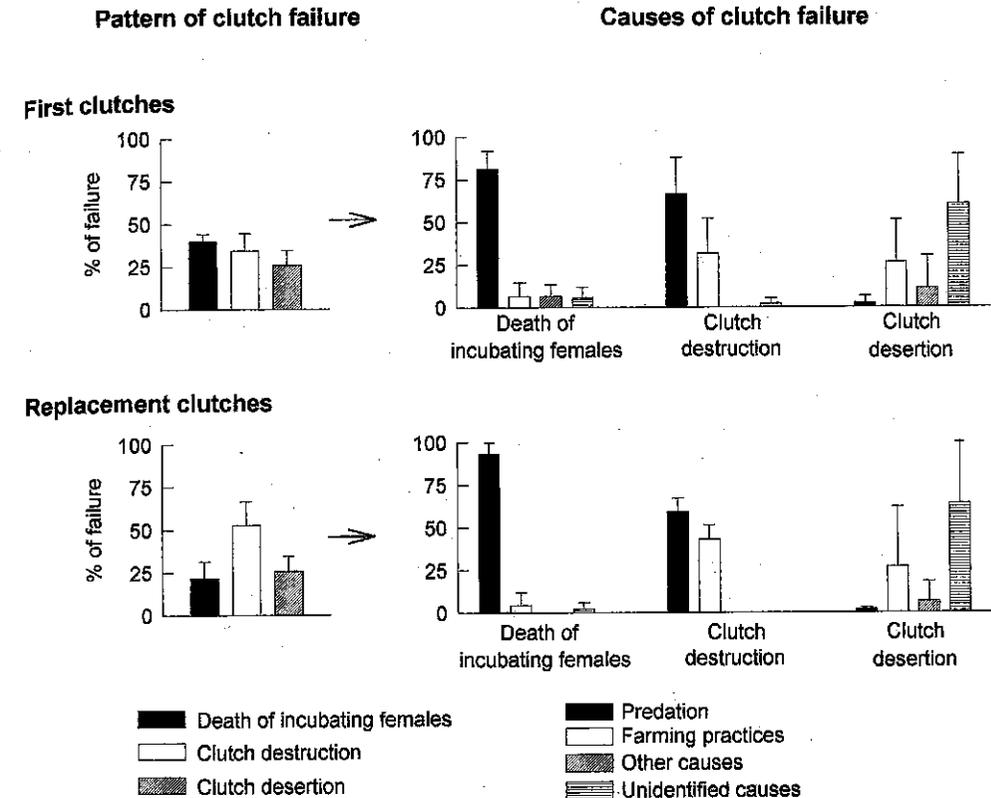- Farming practices
- Other causes
- Unidentified causes

Figure 1: Pattern of clutch failure and cause of clutch failure ("other causes" includes weather condition) of grey partridge, *Perdix perdix*, in relation to nesting attempt. Causes of clutch failure are detailed for each pattern of clutch failure. Mean ± standard error across ten study areas in North-Central France, 1995-1997. Total $n = 407$ first clutches and 141 replacement clutches. Number of clutch failures: 181 first clutches and 89 replacement clutches.

Figure 1 : Modalités de perte (par mort de la poule couveuse – en noir -, destruction des œufs – en blanc -, abandon du nid par la poule - en hachuré) et causes d'échec des pontes (prédation de la poule et/ou des œufs – en noir -, pratiques agricoles – en blanc -, autres causes dont les conditions météorologiques – en hachuré -, et causes non identifiées – en hachures horizontales) de perdrix grise, *Perdix perdix*, en fonction du type de ponte (premières pontes ou pontes de remplacement). Les causes d'échec sont détaillées par modalité de perte. Moyenne ± erreur standard pour dix sites d'étude du Centre-Nord de la France, 1995-1997. Effectif total $n = 407$

First clutches

n = 181

Causes of failure
- ■ Predation on incubating females
- ▨ Predation on eggs
- ☐ Farming practices
- ▧ Other causes
- ☐ Unidentified causes

33%, 25%, 18%, 7%, 17%

Replacement clutches

n = 89

19%, 26%, 38%, 6%, 11%

Egg predators

n = 46

Red fox
■ Mustelids
☐ Unidentified carnivore
▧ Corvids
▨ Unidentified species

37%, 47%, 7%, 7%, 2%

n = 23

26%, 4%, 22%, 48%

Farming practices

n = 33

■ Watering-irrigation
☐ Spraying
▨ Unidentified machine operation
☐ Cutting set-aside
▨ Cutting fodder crops
☐ Harvesting cereals
▨ Harvesting other crops
▨ Cattle

18%, 3%, 18%, 3%, 34%, 9%, 9%, 6%

n = 34

3% 6%, 9%, 6%, 12%, 46%, 18%
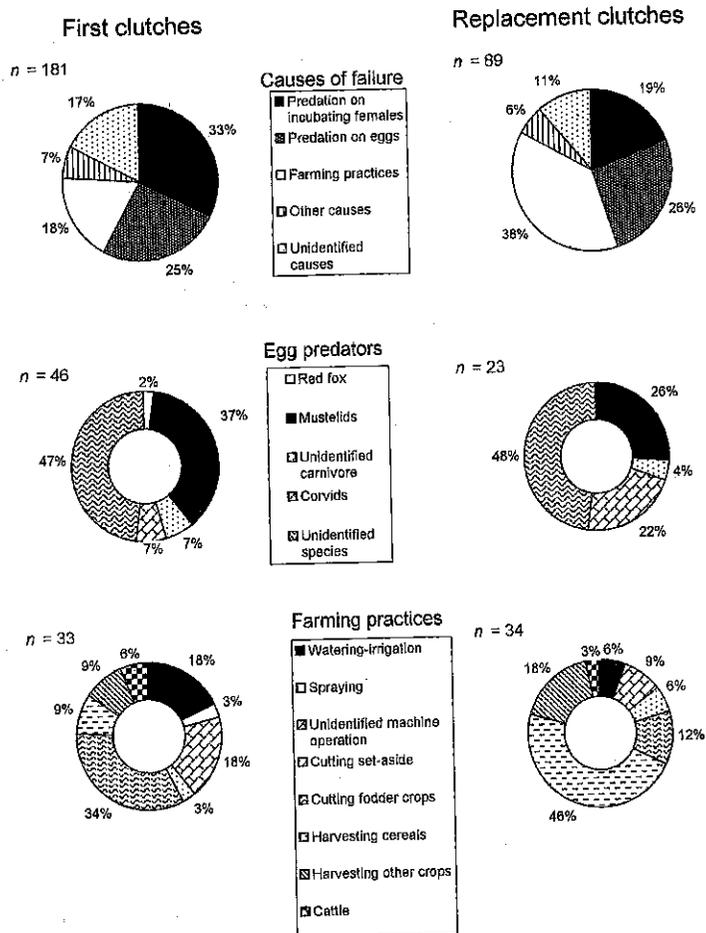
Figure 2: Distribution (%) of causes of failure of first and replacement clutches of grey partridge, Perdix perdix. Putative predators of eggs (i.e., not including predators of incubating females; information about predators of female partridges is given in BRO et al., 2001) and farming practices (whereby incubating females are killed and/or clutches destroyed) are detailed. Ten study areas in North-Central France, 1995-1997. Total n = 407 first clutches and 141 replacement clutches.

Figure 2 : Distribution (%) des causes d'échec des premières pontes et des pontes de remplacement de perdrix grises, Perdix perdix. Les prédateurs supposés des œufs (ceux des poules perdrix non inclus; voir BRO et al., 2001) et les pratiques agricoles (tuant les poules couveuses et/ou détruisant les œufs) sont détaillés. Dix sites coles (tuant dans le Centre-Nord de la France, 1995-1997, effectif total n = 407 premières pontes et 141 pontes de remplacement. Causes de perte : prédation des poules couveuses, prédation des œufs, pratiques agricoles, autres causes, causes non identifiées. Prédateurs des œufs : renard, mustélidés, carnivore non identifié, corvidés, prédateur non identifié. Pratiques agricoles : arrosage-irrigation, traitement

Predators of incubating females (n = 76 predation cases) were red foxes (34%), mustelids (28%), domestic cats (4%), and some raptors (13%) – supposed to be hen harriers, Circus cyaneus (see BRO et al., 2001). Unidentified mammalian carnivores accounted for 17% of female losses and unidentified predators for 4%. The main predators of clutches (n = 69 predation cases) were carnivores: mustelids (33.3%), red fox (1.5%), domestic cats (1.5%) and unidentified carnivores (4.3%). Predation attributed to corvids (carrion crow, Corvus corone corone) represented 11.6% and to hedgehogs, Erinaceus europaeus, 7.2%. Predator species could not be identified in 40.6% of predation cases (Figure 2).

The main cause of clutch failure due to **farming practices** was harvesting whereby many clutches were destroyed (Figure 2). To a far lesser extent, irrigation caused clutch desertion. The impact of farming practices on clutch success depended upon the crops chosen by partridges to nest in (see below).

Most **other causes** of clutch failure were poor weather conditions (10 out of 17 cases). Indeed, after heavy rains some clutches were found deserted. We assumed that these clutches had been flooded and were then deserted by the females (Figure 2). This cause of clutch loss globally represented a small proportion of the losses but locally (i.e., where storms occurred) might lead to high losses and decreased clutch success.

III.3. CLUTCH FATE IN RELATION TO NESTING HABITAT

The pattern of clutch fate (success v failure due to predation – on incubating females and clutches – and farming practices) varied simultaneously between clutch type and across nesting cover (interaction "fate * clutch type * nesting cover": $\chi^2_{10} > 50, p < 0.001$, pooling study areas for sample size reasons; Figure 3). Clutch fate was strongly dependent upon nesting cover for both first ($\chi^2_{10} = 46.13, p < 0.001$) and replacement ($\chi^2_{10} = 24.50, p = 0.006$) clutches.

Success rate of first clutches (Figure 3) was highest in cereals (66%, n = 232) and lowest in fodder crops (23%, n = 13) and meadows (18%, n = 11); it was intermediate in "other crops" (50%, n = 13), linear features (46%, n = 46) and set-asides (45%, n = 20). Although cereals appeared as the best cover, the variation in the amount of cereals across study areas was not significantly correlated with the variation in the success of first clutches ($\chi^2_1 = 0.57$, n.s., one-tailed weighted analysis).

Contrarily to first clutches, the success rate of replacement clutches (Figure 3) was highest in the other crops (52%, n = 27; mainly in sugar beet and pea; BRO et al., 2000a) and set-aside (45%, n = 11) whereas it was poor in cereals (29%, n = 45) and linear features (29%, n = 24). All replacement clutches failed in meadows (n = 3) and fodder crops (n = 7).

Predation rate on both incubating females and clutches ranged from 23% (n = 13, fodder crops) to 45% (n = 11, meadows) across nesting cover types for first clutches and from 22% (n = 27, "other crops") to 57% (n = 7, fodder crops) for replacement clutches (Figure 3). The failure rate of first clutches due to predation was high (40-45%) in linear landscape features (n = 46), other crops (n = 10) and meadows (n = 11) and moderate (25%) in cereals (n = 232). In linear features (n = 46), predation occurred on clutches and incubating females in equal proportion whereas in cereals (n = 232) females were more sensitive to predation than clutches (Figure 3). The situation was different for replacement clutches: predation rate was high (45-60%) in fodder crops (n = 7), linear features (n = 24) and set-aside (n = 11), and still moderate (24%) in

First clutches

Replacement clutches

Legend:
- ■ Success
- □ Predation on incubating females
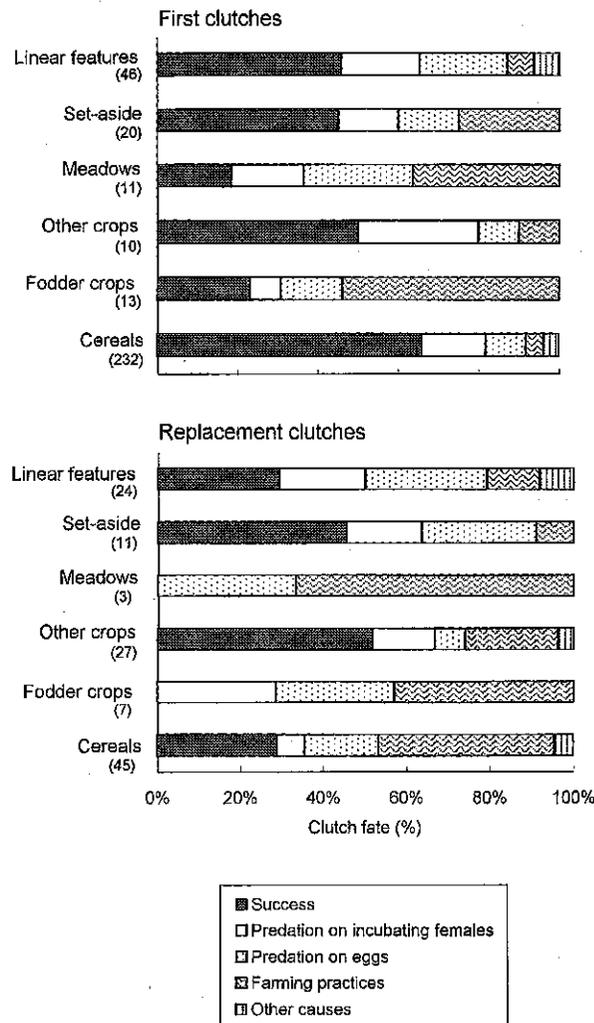- ☐ Predation on eggs
- ▨ Farming practices
- ▥ Other causes

Figure 3: Fate (% success v % failures due to predation on incubating females, predation on eggs, farming practice, and other causes) of first and replacement clutches of grey partridge, *Perdix perdix*, depending upon nesting cover. Figures in brackets refer to sample size, pooling study areas and years. Ten study areas in North-Central France, 1995-1997. Total *n* = 407 first clutches and 141 replacement clutches.

Figure 3 : Devenir (éclosion, échecs par prédation des poules couveuses, par destruction des œufs, par pratiques agricoles, par d'autres causes) des premières pontes et des pontes de remplacement de perdrix grises, *Perdix perdix*, en fonction du couvert de nidification (de haut en bas : éléments linéaires, jachères, pâturages, autres cultures, fourrages, céréales). Les chiffres entre parenthèses correspondent aux effectifs des pontes, en regroupant les 10 sites d'étude du Centre-Nord de la

Replacement clutches were slightly more sensitive to predation than females (in cereals, linear features; Figure 3).

Clutches laid closer to field margins (see Figure 3 *in* BRO *et al.*, 2000a) were not more likely to be depredated (χ^2_1 < 0.01, p = 0.462, one-tailed test; test performed with clutches laid in cereals for sample size reason, pooling first and replacement clutches). The predation rate on clutches was roughly constant with regard to the nearest distance to field margin: ≤ 1m: 29% (n = 31),]1–5m]: 32.7% (n = 49),]5–10m]: 24.6% (n = 61),]10–15m]: 25% (n = 40), ≥ 15 m: 21.9% (n = 96).

The global impact of **farming practices** on first clutches (n = 407) was moderate, less than 10% of first clutches were destroyed directly and indirectly (through the death of incubating females). The most risky covers were fodder crops, meadows and CAP set-aside (Figure 3). Replacement clutches (n = 141) suffered more (29%) from farming practices, especially in cereals, other crops and fodder crops (Figure 3).

In cereals, harvesting in July was the main cause of destruction of clutches, involving mainly replacement clutches (42% of replacement clutches, n = 45) and a few late first clutches (3% of first clutches, n = 232). Irrigation in May–June in intensive cereal production regions caused clutch desertion (4 cases of failure of first clutches out of 10 cases due to farming practices).

In sugar beets (one of the "other crops"), farming disturbance was due to irrigation and caused desertion of some replacement clutches.

In fodder crops, clutches mainly suffered from hay and silage cutting in June that affected both first (7 out of 13 clutches) and replacement clutches (3 out of 7 clutches). As for fodder crops, clutches laid in set-aside suffered from cutting from late May to mid-July. The few clutches in pastures were mainly destroyed by cattle.

The **other causes** of nest failure were highway maintenance and road traffic. Some clutches laid on banks or roadsides were destroyed by highway maintenance (mowing tall weeds in late June – early July for safety reasons), and some hens were killed by cars.

III.4. PREDATION RATE IN RELATION TO PREDATOR ABUNDANCE

For first clutches the failure rate due to predation ranged from 19% (A, n = 41) to 54% (C, n = 26) across study areas, and for replacement clutches from 20% (D, n =15) to 67% (F, n = 6). Failure of clutches due to predation was caused directly by destruction of eggs or indirectly by death of incubating females.

The predation on incubating females v clutches did not differ with clutch type (χ^2_1 = 1.96, n.s.; Figure 2).

The predation rate on incubating females did not vary significantly between clutch type and across study areas (interaction "clutch type * study area": χ^2_9 = 5.08, n.s.; clutch type: χ^2_1 = 2.7, n.s.; study area: χ^2_9 = 14.42, n.s.; range 8-27% for first clutches and 7-21% for replacement clutches). The predation rate on clutches varied across study areas depending upon clutch type (interaction "clutch type * study area": χ^2_9 = 26.06, p = 0.002). The predation rate on first clutches varied across study areas [χ^2_9 = 44.18, p < 0.001, range between 0% (area F, n = 26) and 46% (area C, n = 26)], whereas the predation rate on replacement clutches did not vary significantly across study areas (χ^2_9 = 13.72, n.s.,

rate across study areas was significantly correlated with the abundance of mustelids (χ^2_1 = 5.76, p = 0.008, one-tailed weighted test; Figure 4), whereas the abundance of red foxes was not a significant correlate (χ^2_1 = 0.27, n.s.).

The abundance of mustelids was correlated to habitat structure (presence of pastures, diversity of crops and field size), being more abundant in traditional farmland than in open plains of cereals (BRO, 1998). However, the relationships were linked to one particular study area, H, a landscape criss-crossed by hedges.
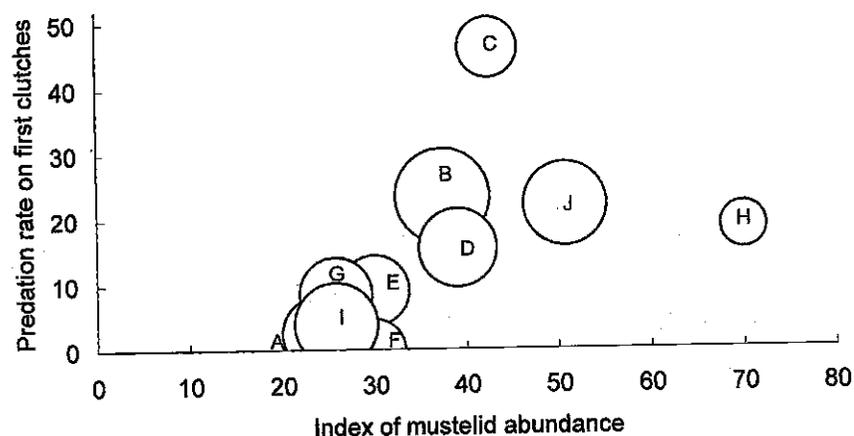
Figure 4: Correlation between the predation rate on first clutches of grey partridge, *Perdix perdix*, and mustelid index of abundance. Letters refer to study areas, and circle diameters to the weight of each observation (recorded sample size of clutches, for instance, I circle diameter refers to 52 clutches). Mustelid abundance index is calculated by the number of positive transects. Ten study areas in North-Central France, 1995-1997, total n = 407 first clutches.

Figure 4 : Corrélation entre le taux de prédation sur les premières pontes de perdrix grises, *Perdix perdix*, et l'indice d'abondance des mustélidés. Les lettres se réfèrent aux sites d'étude, les diamètres des cercles aux poids relatifs des différentes observations (effectifs des nids suivis, par exemple le diamètre du cercle I se réfère à l'effectif 52). L'indice d'abondance des mustélidés correspond au pourcentage de transects positifs. Dix sites d'étude dans le Centre-Nord de la France, 1995-1997. Effectif total n = 407 premières pontes.

IV. DISCUSSION

This work is part of an extensive study of the grey partridge, and is based on recent data collected in contrasting types of arable farmland in North-Central France. It is an update of our knowledge of nesting ecology by identifying and quantifying the causes of clutch failure under different farming regimes and pred-

We found that clutch losses could be particularly high (70%) depending upon areas. When comparing our figures to those reported by AUBINEAU (1981) and BRUN (1991) in the 1970-1980s and reviewed by BIRKAN and JACOB (1988) in North-Central France, it seems that the failure rate of clutches has increased. However, such high clutch losses have been reported in other countries (reviews in POTTS, 1980; AUBINEAU, 1981; BIRKAN and JACOB, 1988).

Our data clearly show that the main proximate cause of the failure of first clutches is predation, with farming practices being secondarily important, whereas replacement clutches suffered more from farming practices v other causes than first clutches. However, the relative balance of failure due to predation v farming practices varied only moderately in space, suggesting that the differences in nest success rather result from a global risk of failure than a factor in particular. The fate of clutches highly depended upon nesting cover used by partridges – and related risks of farming destruction and predation. Thus, to be efficient management should address these points.

Our most original result is the correlation between the spatial variation of the first clutch-predation rate and the spatial variation of mustelid abundance. However, this correlation does not demonstrate a causal relationship. It could reflect a convergence of choices for the same habitat by partridges (for instance choice of nesting cover, BRO et al., 2000a, depending upon cover availability), and by mustelids. Nevertheless, in practice, the relation suggests that reducing the abundance (or trapping near the most risky nesting cover) of targeted species like the stone marten might reduce clutch losses, at least on areas where this very concern has been identified.

Farming practices such as irrigation and harvesting operations occur in most cover types during the incubating period of the grey partridge, so that even the most suitable cover may turn into an ecological trap, especially for replacement clutches. According to POTTS (1980) review, mowing could account for 10–90% of clutch losses depending upon studies. This is a general point of concern for ground-nesting birds living in farmlands (TUCKER, 1997).

Our study provides four main results on the relation between clutch success rate and nesting cover.

1) We confirm that the preferred nesting cover, cereals (BRO et al., 2000a), is also the best cover for first clutches (despite desertion cases due to irrigation as previously reported, e.g. BIRKAN et al., 1990; SERRE et al., 1995), but the destruction rate of replacement clutches due to harvesting is significant.

2) Clutches laid in the second preferred nesting cover, linear landscape features (BRO et al., 2000a), suffer from predation and to a lesser extent from weed management. Although this dilemma has been raised numerous times, it could be solved in practice by concentrating trapping efforts on these particular landscape features. The question is to know whether such local trapping could be efficient.

3) From a global point of view, the application of the set-aside scheme did not appear (in 1995-1997) to be beneficial to clutch success because cutting occurred during the incubation period. Although hunter associations have advocated the benefits for wildlife of the "Environment and wildlife" option (prohibition of mowing, weed control by cutting replaced by chemical control – e.g. RAMEAU and CITRON, 1996) while providing financial incentives, this option has only been adopted for a small proportion of set-aside land (1.7% in 1995; ARNAUDUC, 1996).

4) For the same reasons, fodder crops such as lucerne or clover were not a favourable type of nesting cover despite being attractive (e.g. PEETERS and DECAMPS, 1998). This result has been well documented elsewhere (e.g. BARBIER,

V. MANAGEMENT IMPLICATIONS: STRATEGY FOR GREY PARTRIDGE CONSERVATION UNDER THE "CTE" SCHEME

Detailed research studies on the grey partridge in western Europe have identified the main threats to this species, which led to prescribe both wise management of target-predator populations and changes in farming practices for habitat management as remedial actions to alleviate clutch losses. Predation rate may likely be reduced directly by controlling predator abundance. The seasonal local control of targeted predator species (ideally identified in a preliminary diagnosis survey) could constitute wise management of predator presence. However, the question of the impact of predator control on population dynamics of the prey is still under debate despite solid scientific research on this topic. The experiment conducted in England by the Game Conservancy Trust (GCT) produced substantial results both on autumn and spring densities of partridges (TAPPER et al., 1996). One could argue that such intensity of predator control could only be achieved under experimental conditions and did not correspond to the norm for large areas. Indeed, other similar experiments conducted elsewhere did not lead to convincing results (SERRE et al., 1995; review in CÔTÉ and SUTHERLAND, 1997). However, recent evidence indicates that motivated people reduce red fox density over large areas (GCT, 1998) despite the need for continuous and high density over large areas (GCT, 1998) despite the need for continuous and high intensity control (HEYDON and REYNOLDS, 2000). Less intensively, trapping could be focused on particular features known, on the one hand, to be suitable nesting cover for grey partridge (field margins and linear landscape features) and, on the other hand, used by predators (carnivores such as the stone marten travel along linear items to find their preys; e.g. LÉGER, 1996). If focused trapping could provide satisfactory results, it would be efficient because efforts would be concentrated on high-risk areas for nesting partridges.

Harvesting and irrigation are the two main farming operations affecting grey partridge clutches. An efficient remedial action would be to delay/suppress these farming operations in field margins where most clutches are located (BRO et al., 2000a). This measure is not unrealistic in the context of the new orientation of the European Union's Common Agricultural Policy (CAP). Indeed, owing to current surpluses and increasing environmental problems (e.g., pollution of soil and water, endangered species), the CAP has recently focused on the environmental aspects of agriculture and provides financial incentives for farmers ronmental aspects of agriculture and provides financial incentives for farmers that voluntarily address these concerns. In France, this European directive is applied within the national scheme 'Contrat Territorial d'Exploitation' (CTE). Different measures in favour of wildlife such as planting hedges or strip covers, introducing supplementary crop types, simplifying ploughing, dividing large fields, improving the environmental value of set-aside, etc. are proposed to farmers through a contract with the ministry of Agriculture. All options are granted (from 300 – 4,000 FF/ha/year) to compensate for the loss of income, the additive work or cost (MINISTÈRE DE L'AGRICULTURE ET DE LA PÊCHE, 1999). To maximize the benefits from this scheme, management guidelines must be based on scientific research, be effective for wildlife, and acceptable by farmers in terms of ease of implementation and economics - to compete internationally farming must indeed remain profitable.

Within this framework, which is a contextual policy, our results suggest three measures to reduce clutch destruction/desertion due to farming.

al., 1999; BRO et al., 2000a). This means no pesticides, irrigation or cutting. This could be achieved in the context of the CTE scheme by establishing grassy or cereal-based bird-cover strips located either at field boundaries close to lanes or in the middle of large fields (to create suitable nesting sites) (options 14.2, 14.3 of the CTE scheme; MINISTÈRE DE L'AGRICULTURE ET DE LA PÊCHE, 1999). These boundaries could incorporate "conservation headlands" (option 16.2) to provide, in addition to undisturbed nesting cover, insect-rich chick-feeding habitat (selective herbicides, no insecticides after mid-March; GCT, 1995). Rotational set-aside strips and conservation headlands have previously been shown to improve reproductive success of grey partridges (e.g., BLAKE and DOWELL, 1992). When/where measure (1) cannot be applied, stubbles should be cut at a minimum height of 20 cm above ground to preserve incubating females and eggs.

2) Implement "Environment and Wildlife" set-aside (MINISTÈRE DE L'AGRICULTURE ET DE LA PÊCHE, 1996; options 14.1, 14.3, 16.4, 16.6 of the CTE scheme) instead of traditional (e.g. BESNARD, 1996) or industrial options. Weed plants are controlled by selective herbicides (e.g. RAMEAU and CITRON, 1996).

3) In regions where fodder crops are abundant, a network of cereal-based mixture strips could be established around fodder crop as alternative nesting habitat (BARBIER, 1979); these strips should be managed as in (1). The two alternatives for maintenance are: to mow field margins early (before mid-May) or late (after 20 July) with no farming operations between these two dates (adaptation of the 14.4 option), and to adjust cutting height at 10-15 cm above ground (BARBIER, 1979).

These measures would help to reduce clutch failure. The issue is whether the widespread application of these measures is realistic from a social and economic point of view. Assuming that incentives are/will be attractive enough for intensive arable farms, such a policy offers an excellent opportunity to assist the grey partridge and other wildlife in cereal ecosystems.

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APPENDIX (NEXT PAGES)

Description of data set. Sample size, clutch size and clutch fate of first and replacement clutches of grey partridges, *Perdix perdix*, and predator abundance are given for each study area. North-Central France, 1995-1997.

ANNEXE (PAGES SUIVANTES)

Données concernant les premières pontes, les pontes de remplacement, les troisièmes pontes, les pontes de rang indéterminé de perdrix grises, *Perdix perdix* et l'abondance des prédateurs, suivant dix sites d'étude (A-J) du Centre-Nord de la France, 1995-1997.
Nombre total de pontes, nombre de pontes réussies, taille de ponte, nombre de pontes ratées, au devenir inconnu, désertées à cause du radiopistage. Pertes de pontes par mortalité des poules couveuses, destruction des œufs ou abandon du nid. Causes de perte de ponte : prédation sur poule couveuse, prédation sur œufs, pratiques culturales, autres causes, causes non identifiées. Abondances des mustélidés en pourcentage de transects positifs, et de renards en individus par 10 km.

	Study area										Total
	A	B	C	D	E	F	G	H	I	J	
First clutches											
No. of clutches	44	67	27	46	36	28	39	16	52	52	407
No. of successful clutches	26	26	10	33	17	13	20	5	31	21	202
Clutch size (m ± SE)	10.3 ± 0.8	11.2 ± 0.7	12.4 ± 1.7	11.6 ± 0.6	13.8 ± 0.8	13.4 ± 0.7	13.6 ± 0.7	13.2 ± 1.2	12.2 ± 0.8	11.6 ± 0.7	
	(22)	(25)	(9)	(32)	(17)	(12)	(20)	(5)	(26)	(18)	
No. of failed clutches *	15	38	16	12	16	13	15	11	21	24	181
No. of clutches with unknown fate	3	3	0	0	1	2	1	0	0	1	12
No. of clutches deserted due to radiotracking	0	0	1	1	2	0	2	0	0	6	12
Pattern of clutch failure											
Death of incubating females	6	17	2	3	7	9	4	5	12	8	73
Clutch destruction	1	13	12	5	7	1	5	5	2	11	62
Clutch desertion	8	8	2	4	2	3	6	1	7	5	46
Causes of clutch failure											
Predation on incubating females	6	13	2	3	4	6	3	4	11	7	59
Predation on eggs	1	12	11	5	2	0	2	3	1	9	46
Farming practices	3	5	2	0	5	3	6	3	3	3	33
Other causes	3	2	0	0	1	2	0	1	1	2	12
Unidentified causes	2	6	1	4	4	2	4	0	5	3	31
Replacement clutches											
No. of clutches	13	15	13	16	14	6	17	8	19	20	141
No. of successful clutches	3	7	3	8	4	0	6	2	7	6	46
Clutch size	5.0 ± 1.2	6.0 ± 0.9	11.0 ± 1.0	7.2 ± 1.0	12.0 ± 2.1	/	9.4 ± 1.0	11.5 ± 1.5	10.0 ± 1.7	9.0 ± 1.1	
No. hatched eggs, m ± SE (n)	(3)	(6)	(3)	(6)	(4)	/	(5)	(2)	(7)	(6)	
No. of failed clutches *	9	7	9	7	10	6	10	6	12	13	89
No. of clutches with unknown fate	0	0	0	0	0	0	0	0	0	0	0
No. of clutches deserted due to radiotracking	1	1	1	1	0	0	1	0	0	1	6
Pattern of clutch failure											
Death of incubating females	1	1	2	2	2	1	4	1	3	3	20
Clutch destruction	5	3	7	3	7	4	5	4	0	7	45
Clutch desertion	3	3	0	2	1	1	1	1	9	3	24
Causes of clutch failure											
Predation on incubating females	1	1	1	2	2	1	3	1	2	3	17
Predation on eggs	4	1	2	1	3	2	1	4	1	4	23
Farming practices	3	2	4	1	5	2	5	1	7	4	34
Other causes	1	1	0	3	0	0	0	0	0	0	5
Unidentified causes	0	2	2	0	0	1	1	0	2	2	10
No. third clutches	0	1	1	2	1	0	0	1	0	2	8
No. of "unclassified" clutches	1	1	2	0	0	0	0	0	0	3	7
Predator abundance											
Mustelids (% positive transects)	24.1	37.5	42.5	39.1	30	30	25.8	70	25.8	50.8	/
Red foxes (ind. / 10 km)	0.247	0.220	1.537	2.117	1.057	1.080	0.510	2.590	0.400	0.810	/

*Excluding desertion due to radiotracking.
*Désertions dues au radiopistage exclues.

RÉUSSITE DES NIDS DE PERDRIX GRISES *(PERDIX PERDIX)* DANS LES AGRO-ÉCOSYSTÈMES DU CENTRE-NORD DE LA FRANCE, RELATION AVEC LE COUVERT DE NIDIFICATION ET L'ABONDANCE DE PRÉDATEURS

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RÉSUMÉ

Nous avons suivi 1 009 poules perdrix grises, Perdix perdix, sauvages par radiopistage de mars à septembre sur dix sites d'étude contrastés dans le but d'identifier et de quantifier les causes d'échec des nids. Nous avons noté le devenir de 407 premières pontes et 141 pontes de remplacement. Parallèlement, nous avons estimé l'abondance des renards, Vulpes vulpes, et des mustélidés, Mustelidae, et noté l'habitat des sites de nidification. Le taux de succès des pontes a varié significativement entre les sites d'étude (de 31%, n = 16, à 73%, n = 46) pour les premières pontes (p = 0,013), mais pas pour les pontes de remplacement (de 0%, n = 6, à 53%, n = 16). Les céréales ont constitué le meilleur couvert pour les premières pontes (taux de succès de 66%, n = 232) tandis que les pontes de remplacement y ont souffert des moissons en juillet (taux de succès de 29%, n = 45). Cependant, la variation du taux de succès des premières pontes entre sites d'étude n'était pas corrélée à la variation de l'importance des céréales dans l'assolement. La principale cause d'échec des premières pontes (n = 150 cas d'échecs avec cause identifiée) a été la prédation (70%), suivie par les pratiques agricoles (22%). Les pontes de remplacement (n = 79 cas d'échecs avec cause identifiée) ont échoué du fait de la prédation (51%) et des pratiques agricoles (43%). Les carnivores terrestres (renard, mustélidés et chat domestique) ont été responsables de 66% des cas identifiés de prédation sur les poules couveuses (n =76) et de 36% des œufs directement sur œufs (n = 69). Le taux de prédation des premières pontes était positivement corrélé à l'abondance des mustélidés (p = 0,008), mais pas à celle des renards. Le taux de prédation a été particulièrement élevé (46%) dans les éléments linéaires du paysage (n = 46). Les résultats obtenus justifient l'usage d'un contrôle localisé de certaines espèces de mustélidés pour protéger des nids de perdrix, en complément de mesures de gestion des bords de champs, dans le cadre des nouvelles orientations de la PAC déclinées en France par le programme "Contrat Territorial d'Exploitation", avec pour objectif de préserver la perdrix grise dans les régions de céréaliculture intensive.

EFFICACY AND SELECTIVITY OF HARE (*LEPUS EUROPAEUS*) " BOX TRAPS "

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ABSTRACT

The choice of a capture technique depends on the biology of the species and the problem to be studied. It also depends on its efficiency, the method's cost and selectivity, and the ensuant risks of mortality. Hares, Lepus europaeus, were captured with box traps in two study areas (area 1, Bellay-en-Vexin, Val d'Oise, and area 2, Chareil-Cintrat and Montord, Allier). The 13-km² study area 1 is typical of a region of intensive cultivation and the 17-km² study area 2 of an area of polyculture-breeding. Average size of the fields in area 1 was larger than that of the fields in area 2 (12 ha vs 2 ha), and its landscape was less diversified. Because of the different hunting pressures in each study area, it was possible to single out in each of them two zones with different hare densities (8 and 26 hares per 100 ha in study area 1; 14 and 49 in study area 2). Unbaited box traps with drop gates were set up in open habitats, on bare ground or grounds with low vegetation. Preliminary tests carried out in 1985 and 1986 showed the greater efficacy (number of captures/100 nights × traps) of large box traps (L × w × h: 100 × 40 × 40 cm) with respect to small ones (100 × 30 × 30 cm) (3.3 vs 1.2, P < 0.0001). Large box traps (the only ones used between 1987 and 1996) were more effective on study area 1 (5.3: 247 hares captured in 4,636 nights × traps in May-October 1987-1990) than on study area 2 (2.3: 186 hares in 7,938 nights × traps in May-October 1994-1996). Trap mortality rate and recapture rate both amounted to 3% (n = 433). Trapping yield was 0.43 captured hare/trapper hour on area 1 and 0.19 on area 2, i.e. three to seven times higher than the yield obtained for captures by beats into nets. An analysis of the effect of " trapping area ", " luminosity at night ", " soil humidity ", " hare density in spring " and the " period of trapping " on capture success, was carried out by fitting log-linear models to the data and the application of Akaike's information criterion (A.I.C). In all areas, the degree of luminosity at night had a greater impact on trapping success than the degree of soil humidity. On both areas, trapping became more efficient with greater night luminosity (a 2.2 to 5.0 average increase). In contrast, the effect of hare density on capture success varied by area. Because of this result we were compelled to analyze in addition, and one by one, the influence of the other variables in each trapping area. On each of these two areas, trapping efficiency increased over the seasons and with night luminosity (which increased on average from 2.1 in May-June in dark nights, to 7.4 in September-October in clear