PESTICIDE USE ON CEREALS AND THE SURVIVAL OF GREY PARTRIDGE CHICKS: A FIELD EXPERIMENT

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SUMMARY

(1) A field experiment was undertaken to test whether the herbicides and fungicides used on cereal fields reduce the chick survival of grey partridges.

(2) Mean brood size and the abundance of insects as food for partridge chicks were significantly higher where small areas of cereal fields were left unsprayed than on completely sprayed fields.

(3) The implications of these findings for the conservation of the grey partridge are discussed.

INTRODUCTION

The grey partridge (*Perdix perdix* L.) population of Britain has been declining since 1945 (Potts 1980) and Blank, Southwood & Cross (1967) found that the key factor causing changes in a population in Hampshire was chick mortality. Southwood & Cross (1969) established that chick survival was related to insect abundance. Following this, Potts (1980) developed a simulation model of grey partridge population dynamics incorporating data from many areas, which identified the abundance of arthropods in cereal crops in June as the main factor influencing chick survival. Green (1984) showed that grey partridge broods foraged for insects in the edges of cereal fields where arthropods and weeds were most abundant.

Cereal crops are sprayed with herbicides and fungicides to reduce yield loss caused by weed competition, grain contamination and the spread of fungal diseases. However, these pesticides also have an adverse effect on some cereal insects (Southwood & Cross 1969; Potts & Vickerman 1974; Vickerman 1974; Sotherton 1982; Vickerman & Sotherton 1983; Sotherton & Moreby 1984), both directly and by removing the weeds on which they feed. Thus, it has been suggested that herbicides and fungicides may remove the prey of partridge chicks and so reduce partridge chick production (Southwood & Cross 1969; Potts 1970, 1980).

In this paper I describe a field experiment designed to test the effect of pesticide use on grey partridge chick production by manipulating spraying regimes on cereal fields. The study is part of a research programme on the effects of pesticides on beneficial insects, game and other wildlife in cereal crops (Rands, Southerton & Moreby 1985).

METHODS

Study area

The study area was part of an arable farm (The Manydown Farm) covering about 11·0 km² of north-east Hampshire. In 1983 some 65% of the ground consisted of cereal crops of which about 45% (237·1 ha) were winter-sown wheat, 18% (93·4 ha) were winter-sown
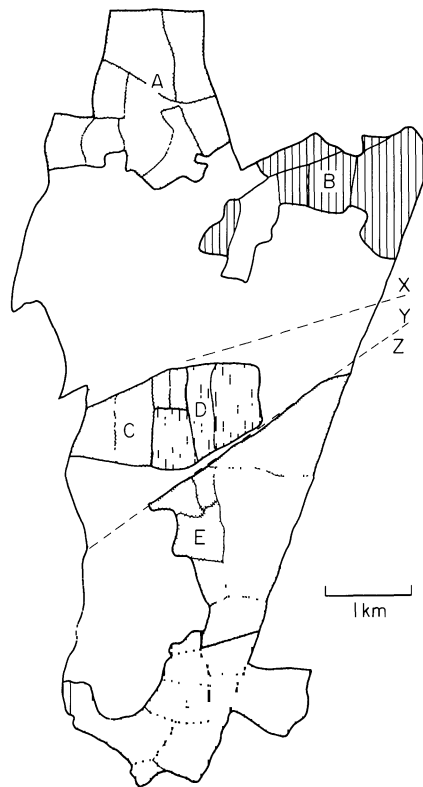
FIG. 1. The study area showing the beats (X, Y and Z) and the plots of fields with sprayed headlands (▓) (A, C and E) and unsprayed headlands (▥) (B, D and F). The blank areas between the plots are a mixture of woodland, grass fields and other non-cereal crops.

barley and 37% (190·4 ha) spring-sown barley. The farm is divided into three beats (X, Y, Z) (Fig. 1), on each of which the predators of game are killed by a different gamekeeper.

For this experiment thirty-seven cereal fields were divided into six trial plots (A–F in Fig. 1), with two plots per beat. A 6 m strip around the edge of every field in one plot of each beat was left unsprayed with pesticides from 1 January 1983. In the other plot of each beat, the entire area of each field was sprayed as normal. Thus, the fields in plots A, C and E (Fig. 1) were sprayed all over while the field edges in plots B, D and F were unsprayed. Plot sizes and cropping are given in Table 1.

The boundaries between sprayed and unsprayed plots were chosen to coincide with natural barriers to partridge movement, such as woods, shelter belts and a railway embankment so as to minimize the likelihood of broods moving between treatments.

Pesticide spraying

During the autumn of 1982 all winter-sown barley fields were sprayed with two herbicides, a fungicide and an insecticide, and spring-sown barley fields were sprayed with a broad spectrum herbicide. No part of any field was left unsprayed.

In 1983 the following applications of pesticides were made. Winter wheat: one grass weed herbicide, one broad-leaved weed herbicide, three fungicides. Winter barley: no herbicides, two or three fungicides. Spring barley: one grass weed herbicide, one fungicide.

TABLE 1. The sizes and cropping of experiment plots of fields in Fig.1.

| | | | | Area (ha) | | |
Beat	Plot	Winter wheat	Winter barley	Spring barley	Total	Unsprayed headland
X	A	55·9	22·1	51·9	129·9	0
X	B	73·7	12·3	8·9	94·9	4·9
Y	C	9·5	0	22·7	32·2	0
Y	D	0	16·7	14·9	31·6	1·9
Z	E	70·7	29·2	7·1	107·0	0
Z	F	27·3	13·1	84·9	125·3	7·1

No insecticides were used and only one field (33·5 ha) was sprayed with a molluscicide. The pesticides used are listed in Appendix I.

Partridge counts

The size and composition of family parties (coveys) were recorded by field counts between 15 August and 5 September. Each field was surveyed from a four-wheel drive vehicle driven systematically across the stubbles. Broods were counted using 10×50 binoculars. Counting was confined to days of calm fine weather and carried out 2–3 h after sunrise and a further 2–3 h before sunset when partridges were actively feeding (see Potts 1980).

Similar counts were carried out in 1980 and 1981 as part of the Game Conservancy's Partridge Count Scheme (see Potts 1980). These are necessary to check whether the experimental and control areas used in 1983 differed in their brood size before the experiment began.

Abundance of chick foods

The insects available to chicks in the sprayed and unsprayed headlands were sampled on 22 and 23 June 1983, the main hatching period for chicks (Potts 1980). One headland in each of the thirty-seven cereal fields was sampled with a $1·0 \times 0·4$ m sweep net, 3 m from the field boundary. Fifty sweeps were made per field edge and samples were sorted and counted as described by Green (1985).

RESULTS

Brood sizes

A total of sixty-eight grey partridge broods were observed in 1983, twenty-nine within plots with unsprayed edges and thirty-nine within fully sprayed plots. The difference in brood distribution reflected the breeding densities of adults in spring (thirty-seven pairs on unsprayed areas, forty-nine pairs on sprayed areas).

Mean brood size on each of the three beats was significantly higher on plots with unsprayed headlands (Table 2). When broods recorded on the three unsprayed plots were pooled and compared with all the broods on sprayed plots, the unsprayed treatments produced significantly higher brood sizes (sprayed: $\bar{x} = 2·15 \pm 0·52$, $n = 39$, unsprayed: $\bar{x} = 6·38 \pm 0·92$, $n = 29$, $t = -4·26$, $P < 0·001$). Brood size observed after cereal harvesting is a product of the mean number of young hatching per successful nest and chick survival rate. Potts (1980) and Green (1984) give methods of calculating chick survival rate from partridge counts, based on the assumption that the mean number of young hatching per successful nest is constant (see Potts 1980). Given this assumption it follows from the results in Table 2 that chick survival rates were significantly higher on unsprayed than on sprayed areas.

TABLE 2. Grey partridge brood size on areas with sprayed and unsprayed cereal headlands (*n* is given in parentheses)

	Mean ($\pm$S.E.) brood sizes	
Area	Sprayed headlands	Unsprayed headlands
Beat X	$2\cdot35 \pm 0\cdot63$ (20)	$5\cdot14 \pm 1\cdot11$ (14)
Beat Y	$1\cdot75 \pm 0\cdot65$ (4)	$10\cdot33 \pm 0\cdot98$ (3)
Beat Z	$2\cdot27 \pm 1\cdot00$ (15)	$6\cdot83 \pm 1\cdot58$ (12)

F between treatments = $22\cdot77$, $P < 0\cdot005$;
F between beats   = $0\cdot65$, N.S.
F interactions   = $2\cdot07$, N.S.

To test for possible differences in brood size between the plots before the 1983 spraying treatments, previous partridge counts for the corresponding areas carried out in 1980 and 1981 (1982 data were incomplete) when all fields were sprayed, were examined (Table 3). No differences were found between plots. Brood sizes were higher throughout the study area in 1980 and 1981 because overall insect abundance was greater (c.f. Potts 1980). Similarly, variations in the proportion of different cereal types within plots (Table 1) did not correlate with changes in brood size, and therefore crop type could not account for the observed differences in chick survival.

TABLE 3. Grey partridge brood size in 1980 and 1981 on the experimental and control plots used in 1983 (*n* is given in parentheses)

Year	Beat	Mean ($\pm$S.E.) brood size	
		Sprayed in 1983	Unsprayed in 1983
1980	X	$7\cdot20 \pm 1\cdot95$ (10)	$7\cdot00 \pm 3\cdot69$ (4)
	Y	$12\cdot00$ (1)	$15\cdot00 \pm 0\cdot0$ (2)
	Z	$8\cdot00 \pm 1\cdot37$ (16)	$9\cdot56 \pm 1\cdot50$ (16)
1981	X	$5\cdot67 \pm 2\cdot29$ (6)	$5\cdot00 \pm 2\cdot23$ (5)
	Y	$6\cdot67 \pm 3\cdot93$ (3)	$0\cdot66 \pm 0\cdot54$ (3)
	Z	$4\cdot94 \pm 1\cdot17$ (19)	$3\cdot50 \pm 0\cdot82$ (16)

1980: F between treatments = $0\cdot30$, N.S.   1981: F between treatments = $2\cdot03$, N.S.
F between beats   = $0\cdot81$, N.S. F between beats   = $0\cdot48$, N.S.
F interaction   = $0\cdot14$, N.S. F interaction   = $0\cdot87$, N.S.

Abundance of chick food

The relative abundance of the various foods of chicks, in both sprayed and unsprayed headlands is given in Table 4. In all groups, except the larvae of sawflies and the lepidopteran, there were significantly higher prey densities where headlands were left unsprayed.

TABLE 4. The abundance of grey partridge chick foods in sprayed and unsprayed headlands

Prey species	Mean ($\pm$S.E.) number of prey items per fifty sweeps ($\log_{10} N + 1$)		*t*	*P*
	Sprayed headlands ($n = 19$)	Unsprayed headlands ($n = 18$)		
Heteroptera	$1\cdot36 \pm 0\cdot13$	$1\cdot90 \pm 0\cdot15$	$2\cdot74$	$<0\cdot02$
Sawfly and lepidopteran larvae	$0\cdot51 \pm 0\cdot05$	$0\cdot61 \pm 0\cdot08$	$0\cdot82$	N.S.
Chrysomelidae and Curculionidae	$0\cdot74 \pm 0\cdot03$	$0\cdot98 \pm 0\cdot09$	$2\cdot42$	$<0\cdot05$
Total prey	$1\cdot53 \pm 0\cdot10$	$2\cdot06 \pm 0\cdot10$	$3\cdot72$	$<0\cdot001$

DISCUSSION

Grey partridge brood size was significantly higher where cereal field headlands were left unsprayed with herbicides and fungicides. This study provides experimental evidence that pesticide use on arable farmland reduces brood size, and hence chick survival, as was indicated by earlier studies (Southwood & Cross 1969; Potts 1970, 1980). Since chicks feed on insects along the edges of cereal fields (McCrow 1980; Green 1984) and the abundance of some of these insects is reduced by herbicides (Cross 1966; Sotherton 1982) and fungicides (Sotherton 1980; Vickerman & Sotherton 1983; Sotherton & Moreby 1984), the adverse effect of pesticides is most likely to be through reducing chick food supplies.

Potts (1980) reported that average chick survival rate had declined in Britain since the 1950s and concluded that this was a major factor responsible for the decline of the grey partridge. To maintain a partridge population, Potts (1971) suggested that brood sizes should average 3·14. The present study recorded mean brood sizes of <3·0 on all areas where cereal fields were completely sprayed, but where headlands were unsprayed, mean brood size was always >5·0 (Table 2). With a continuing decline in chick survival rate (Potts 1980), the further use of pesticides is likely to reduce chick survival below the threshold needed to maintain partridge populations.

Leaving unsprayed strips within cereal fields is potentially useful for grey partridge conservation. Their positioning along the edges of cereal fields is most appropriate since this is the preferred feeding habitat of young partridges (McCrow 1980; Green 1985). Field edges also produce lower cereal yields than any other part of the field so that unsprayed areas adjacent to field boundaries will minimize crop losses. In fact, preliminary results suggest that cereal yields are no lower, at least in the short-term, when headlands are left unsprayed (Rands, Southerton & Moreby 1985).

ACKNOWLEDGMENTS

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APPENDIX 1

The pesticides used on cereal crops during this study.

Grass Weed Herbicides	*Fungicides*
Hytane	Tilt
Arelon	Bayleton
Tolkan	Bayleton CF
	Hispor
Broad-Leaved Weed Herbicides	Sportak Alpha
Swipe	
Cerridor	*Molluscicide*
Brittox	Draza
Harrier	
Malet	

EFFECT OF HEDGEROW CHARACTERISTICS ON PARTRIDGE BREEDING DENSITIES

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SUMMARY

(1) The influence of the quantity and quality of nesting habitat (field boundaries, including hedgerows) on the breeding density of grey and red-legged partridge was examined on ten arable farms in Britain.

(2) The length of permanent field boundary was found to correlate closely with the breeding density of both species of partridge within study farms; between farms it did not.

(3) In a multiple regression analysis the amount of dead grass present in the base of the hedge was the best predictor of grey partridge breeding density within farms after the length of the field boundary was taken into account. A similar analysis for red-legged partridges showed that the amount of nettle present at the base of field boundaries was the only variable related to breeding density after the overall length was taken into account. Between farms, the breeding density of both species was unrelated to the hedgerow characteristics.

(4) The importance of hedges and hedgerow management to partridges is discussed. It is suggested that hedgerow characteristics are important in determining the local spacing of breeding partridges but they may not determine overall population size.

INTRODUCTION

In this paper, the effects of both amount of hedgerow and various aspects of hedge quality on grey and red-legged partridge breeding densities are examined.

The value of hedges to birds on farmland has been the subject of several recent studies in the British Isles. For example, O'Connor (1984) found that the abundance of thirty out of fifty-seven farmland bird species recorded on Common Bird Census plots was closely correlated with hedgerow abundance, and Osborne (1982) showed that the frequency of bird sightings on a study farm in Dorset was correlated with the densities of scrub and hedgerows. Furthermore, Arnold (1983) and Osborne (1984) have both shown that the detailed structure of hedgerows also influences the numbers of birds recorded. Prior to these studies, however, quantitative evidence indicated that hedges were a suboptimal habitat for farmland birds and, consequently, of little value to them (Murton & Westwood 1974).

Hedges are the major nesting habitat for the grey partridge (*Perdix perdix* L.) and the red-legged partridge (*Alectoris rufa* L.) in Britain, and the decline of both species has been attributed, in part, to a loss of suitable nesting habitat as a result of hedgerow removal (Potts 1980). Studies of individually marked pairs of grey partridges in the U.S.A. showed that they spent the majority of their time after pairing in close proximity to nesting cover (Church 1980), while a similar study of red-legged partridges in Britain showed that the proportion of males remaining to breed in an area reflected the distribution of suitable field

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boundaries (Green 1983). Variation in hedgerow 'quality' (physical structure and vegetation characteristics) has also been identified as a factor affecting the suitability of hedges for nesting. For instance, Blank, Southwood & Cross (1967) and Hunt (1974) suggested that 'incomplete' hedges were the best type of nesting cover for grey partridges because of their ground vegetation characteristics. However, no previous studies have attempted to quantify hedgerow quality and relate it to partridge numbers.

METHODS

Study areas

Ten study farms were chosen to represent a range of partridge breeding densities and a variety of habitat types. They were selected from contributors to the Game Conservancy's National Game Census who record annually the numbers of partridges observed on a series of farms throughout Britain (Potts 1980). The study farms ranged from 3·76 to 12·14 km² in area. Further details of the farms are given in Rands (1982).

Each study farm was divided into five or six plots, ranging in size from 1 to 2 km². Where possible, natural barriers to partridge movement, such as woods and shelter belts, were used to define the limits of each plot so as to reduce errors in estimates of breeding density.

Partridge breeding density

The study farms were surveyed from a four-wheel-drive vehicle driven systematically across all fields during the first 2–3 h after dawn and preceding dusk, the times when partridges are feeding and therefore most easily observed (Jenkins 1956). Pairs of partridges were plotted on large-scale maps (1:10 560), which were later used to calculate breeding densities.

Nesting habitat

A set of habitat variables was chosen to describe the structure and characteristics of all potential nesting habitats. These were measured for each field boundary on the ten study farms (1266 boundaries in all) during field surveys carried out between January 5 and March 14. The variables are listed and described in more detail in the Appendix.

In addition to these measures of the quality of nesting habitat, the amount of potential nesting habitat (field boundaries, including hedgerows) was measured to the nearest 5 m from 1:2500 scale Ordnance Survey maps.

RESULTS

Breeding density and length of nesting habitat

Grey partridges occurred on nine of the farms and red-legged partridges on eight. Breeding densities varied from 0 to 45 pairs of grey partridges per km² (range = 31) and from 0 to 35 pairs of red-legged partridges per km² (range = 22). The length of potential nesting habitat ranged from 2·7 to 36·6 km per km², with a maximum within-farm variation of 20·0 km per km².

The breeding density of grey partridges correlated closely with the length per unit area of nesting habitat available on seven out of the nine farms (Fig. 1). This independent variable alone accounted for up to 81% of the variation in grey partridge breeding density.

Red-legged partridge breeding density was significantly correlated with length of nesting
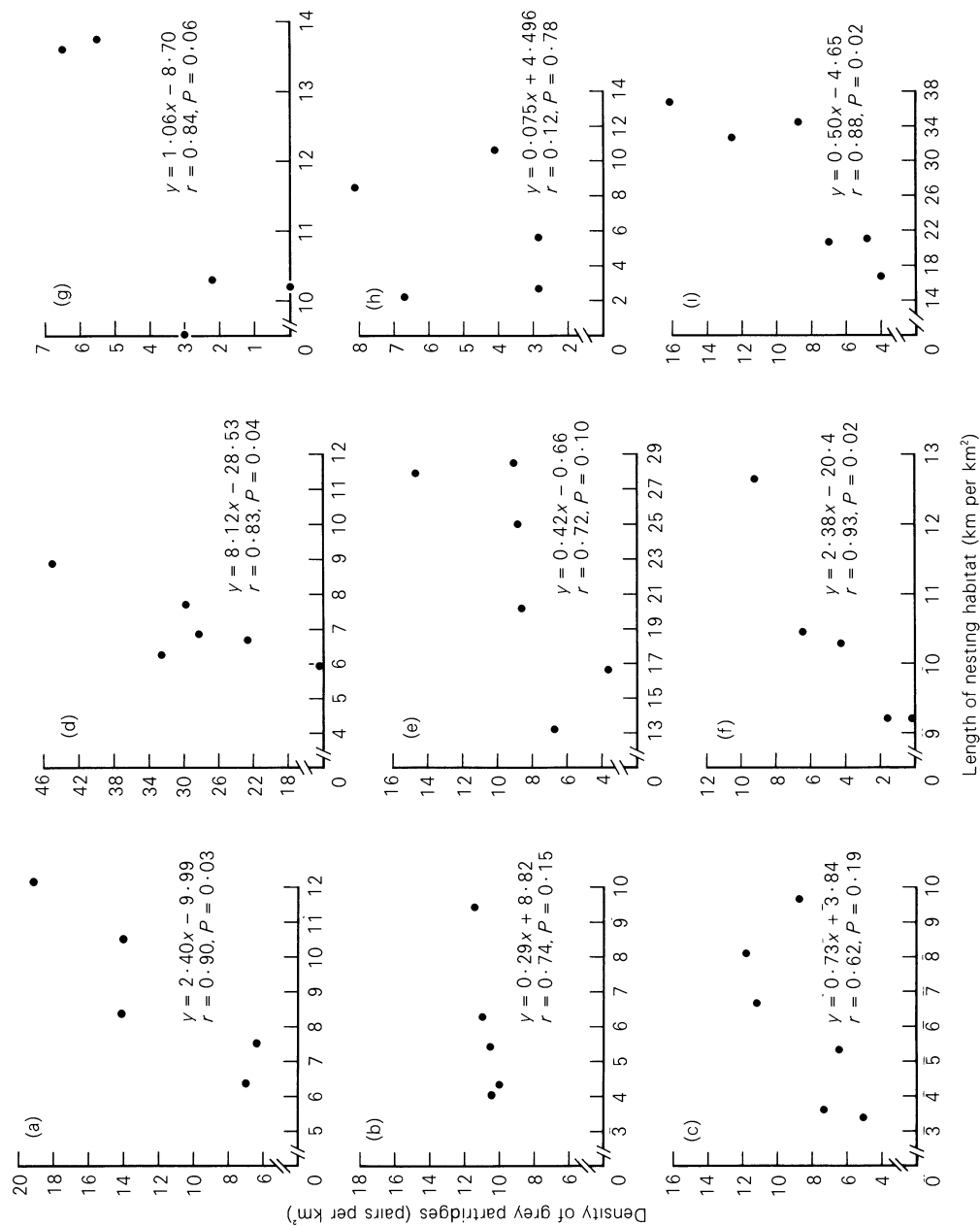
FIG. 1. The relationship between grey partridge breeding density and the amount of hedgerow available as nesting habitat for nine study farms (a–i) in the U.K.
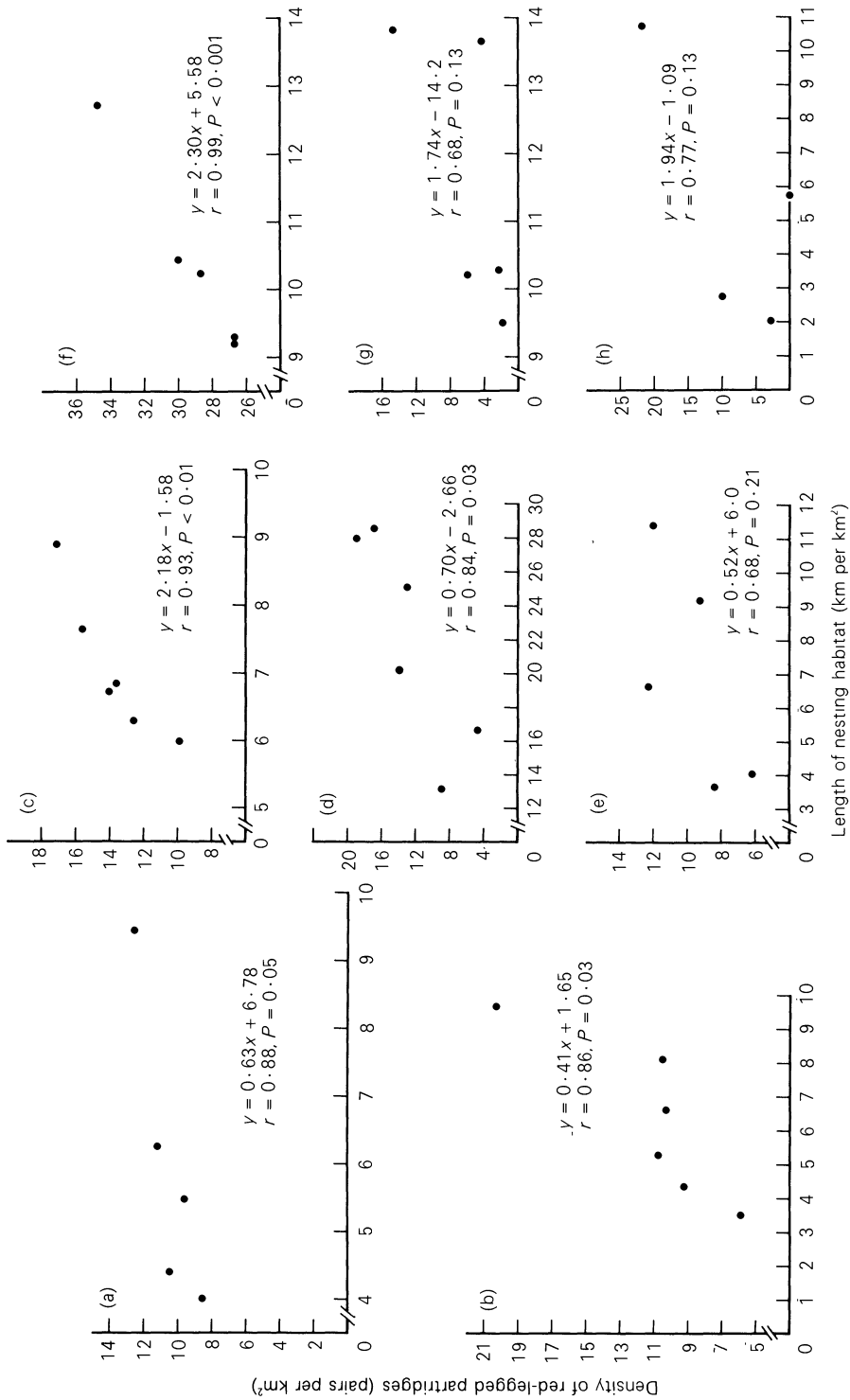
FIG. 2. The relationship between red-legged partridge breeding density and the amount of hedgerow available as nesting habitat for eight study farms (a–h) in the U.K.

habitat on six out of eight farms (Fig. 2). Variation in breeding density between farms was not related to the amount of nesting habitat available for either species (grey partridge: $r = 0.22, P < 0.05, n = 9$; red-legged partridge: $r = 0.07, P < 0.05, n = 8$).

Breeding density and quality of nesting habitat

When considered in isolation, none of the variables chosen to measure the quality of nesting habitat correlated significantly and consistently between farms with the breeding density of either species of partridge.

A stepwise multiple regression analysis of density against all habitat variables shows that, once length of potential nesting habitat has been taken into account, the amount of dead grass present in the base of the field boundary was significantly and positively related to grey partridge breeding density on seven out of nine farms (Table 1). A comparison of the multiple regressions (Bliss 1970) reveals that the partial regression coefficients differed significantly between farms ($F_{24,22} = 15.53, P < 0.001$). Variation in breeding density between farms was not related to variation in hedgerow characteristics.

Multiple regression analysis for the red-legged partridge (Table 1) shows that the amount of nettle *Urtica dioica* L. present in the base of the field boundary was the only variable correlated with breeding density once the length of nesting habitat has been taken into account, and this relationship was statistically significant on only four out of eight farms but again differs significantly between farms ($F_{21,19} = 21.53, P < 0.001$). Variation in hedgerow characteristics between farms did not account for differences in their breeding density of red-legged partridges.

TABLE 1. Stepwise multiple regression analysis of partridge breeding densities in relation to hedgerow characteristics

Farm	Grey partridge R^2 (%)	Partial regression coefficients Hedge length	Partial regression coefficients Dead grass	Red-legged partridge R^2 (%)	Partial regression coefficients Hedge length	Partial regression coefficients Nettle
A	94	3·20*	0·36*		None present	
B	82	0·37*	0·05*	85	0·59	0·04
C	63	1·95	0·15	83	1·74*	0·24*
D	80	9·41*	0·58*	87	2·46*	0·10
E	56	0·28*	0·03*	90	0·98*	1·08*
F	99	1·68*	0·33*	99	2·36*	0·72*
G	62	1·11*	0·63*	98	0·70*	0·71*
H	47	0·58	0·41	48	1·23	1·37
I	93	0·66*	0·45*		None present	
J		None present		84	0·67*	0·10

* $P < 0.05$.

DISCUSSION

The breeding density of grey and red-legged partridges was closely and consistently correlated with the amount of nesting habitat available, in the form of permanent field boundaries (usually hedgerows). This suggests that the partridges are locally distributed in relation to available nesting habitat. The view that hedgerow density, at least in part, determines partridge breeding density is supported by the studies of Church (1980) and Green (1983) who found, for grey and red-legged partridges, respectively, that adult distribution in late spring was related to the distribution of nesting habitat. Both these

workers studied only one or two study areas. In contrast, this study has examined the relationship between nesting habitat and breeding density within ten separate study areas, which exhibited wide ranges of partridge densities and lengths of field boundary.

Although the precise relationship between hedges and partridge density has previously received little attention, it has been widely suggested that the amount of nesting habitat present within a given area is important in determining the extent of pre-breeding emigration from that area (Middleton 1936; Jenkins 1961; Church 1980; Potts 1980; Green 1983). An analysis of dispersal from a range of farms in Britain, including those used in this study, showed that the number of yearlings emigrating every spring from each farm was related to both the quantity and quality of nesting habitat available (Rands 1982).

Grey partridge breeding density was also related to the quality of nesting habitat. The eleven variables chosen to measure habitat quality were selected because previous studies in Britain (Blank, Southwood & Cross 1967) and the U.S.A. (Hunt 1974; Hupp, Smith & Ratti 1980) had suggested that they may influence nesting behaviour. A stepwise multiple regression analysis selected the amount of dead grass at the base of the hedge as the best predictor of breeding density after length of nesting habitat had been taken into account; no other aspect of habitat quality was found to be quantitatively related to grey partridge breeding density. Female grey partridges use dead grass to cover their eggs during the laying period prior to incubation, and the quantity of dead grass was shown to be the single most important variable in predicting where grey partridges choose to nest and the likelihood of a nest being taken by a predator (Rands 1982).

The influence of habitat quality on red-legged partridges was less clear. Multiple regression analysis selected the amount of nettle present at the base of the field boundary as the best predictor of breeding density after length of nesting habitat had been taken into account, but this was only significant on half of the study farms on which there were red-legged partridges. Both Blank (1969) and Rands (1982) have shown that nettle is a preferred nesting vegetation for the red-legged partridge, although no selective advantage was demonstrated in terms of reduced predation risk. From this, the effect of nettle on breeding density is most likely to arise because nettles are chosen as nesting cover. The relationship may be weak because it is difficult for the birds to predict nettle abundance at the time when breeding densities are established. Further work is needed to establish the importance of nettles to red-legged partridges.

It is now widely acknowledged that the number of hedges in Britain has been drastically reduced since the 1940s (see, for example, Pollard, Hooper & Moore 1974; Fuller 1982). Since partridge breeding density is correlated with the amount of field boundary available, this loss of hedges may, in part, be responsible for the decline in Britain of both grey and red-legged partridges (Potts 1980). Furthermore, a change in the methods of hedge management from traditional laying to frequent mechanical trimming has reduced the amount of dead grass present in hedge-bottoms (Rands 1982) and, consequently, has reduced nesting habitat quality for the grey partridge. However, hedgerow characteristics alone do not account for variation in partridge breeding density between farms; in fact, the effect of the quantity and quality of hedgerow available within a farm on breeding density varied significantly between farms. These results suggest that hedges play an important role in determining the local spacing of breeding pairs but that other factors may be more important in controlling overall partridge numbers (see Potts 1980, 1984; Rands 1985).

The controversy over the importance of hedges to farmland bird communities will doubtless continue (for a recent review see O'Connor 1984). Nevertheless, it is clear from this study that two species that depend on field boundaries as nesting habitat are, in Britain,

adversely affected by hedgerow removal. In contrast to songbirds, however, where variations in the structural and vegetational characteristics of the hedge itself have been shown to influence bird densities (Arnold 1983; Osborne 1984), none of the variables chosen to measure hedge quality affected partridges. Instead, the vegetation characteristics at the base of the hedge or field boundary determine the nesting habitat quality and, in so doing, influence their breeding densities. Further work is necessary to establish precisely which features of hedgerows influence which species of bird and to assess how best to manage these hedges to achieve the maximum abundance and diversity of birds on farmland. The approaches adopted here and elsewhere (Arnold 1983; O'Connor 1984; Osborne 1984) are all statistical. Future research should attempt to clarify these studies by experimental manipulation of hedgerows and their characteristics and by measuring the response of bird populations.

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APPENDIX

The habitat variables recorded for each field boundary are defined below (the units of measurement are given in parentheses).

Length	(per km^2)
Width	(m)
Height of bank at base	(m)
Amount of dead grass in ground vegetation	(%)
Amount of nettle in ground vegetation	(%)
Amount of bramble in ground vegetation	(%)
Amount of cover provided by ground vegetation	(%)
Visibility through ground vegetation	(%)
Number of trees	(per km)
Number of gaps	(per km)
Presence of a wire fence	(presence/absence)
Presence of a ditch	(presence/absence)

Field boundary size

Width and height (where a hedge was present) were measured to the nearest 10 cm with a metre rule at three randomly chosen places along each field boundary. Where a hedge was planted on an earth bank (a common practice in much of East Anglia), the height of the bank was also measured.

Ground vegetation characteristics

Five measures were taken to describe the basic composition and density of ground vegetation. Each was measured as the relative proportion of a 2-m length of field boundary at three randomly chosen places along each boundary.

(a) *Amount of dead grass.* Dead grass almost always consisted of last year's growth still attached to its roots. All species were considered together.

(b) *Amount of nettle.* Stinging nettles, *Urtica dioica* L., die back every winter but the dead stems and basal area remain easily recognizable.

(c) *Amount of bramble.* The above-ground parts of bramble, *Rubus fruticosus* L. *sensu lato*, form part of the shrub layer but were only recorded in this survey when contributing to the ground vegetation. This species often provided physical support for stems of dead grass.

(d) *Amount of cover.* Cover is used here to describe all types of vegetation present at ground level and is analogous to Greig-Smith's (1957) 'basal area' when applied to all types of vegetation. It was measured as the proportion of a 2-m length in which a sitting partridge would be concealed by vegetation.

(e) *Visibility through the ground vegetation.* This was measured using a 10 × 12 cm quadrat, held at arm's length 30 cm above ground level and 5 m from the field edge. The proportion of sky seen through the part of the field boundary framed by the quadrat was recorded.

Number of hedgerow trees

The total number of trees (defined as woody stems over 4 m high and greater than twice the height of adjacent shrub vegetation) was recorded for each field boundary.

Number of gaps in the hedgerow

A gap was defined as a distinctive break in the hedgerow shrub vegetation, large enough for a covey of partridges to fly through. In practice, this was taken as approximately the size of a standard five-bar gate (3 m).

Presence of fence and ditches

The presence or absence of a ditch or wire fence was recorded during vegetation sampling.

The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix*

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Summary

1. A 6-year experiment is described which was designed to test whether or not predation control, as practised by traditional and currently legal methods, increases (i) the breeding success and autumn numbers of partridges, and (ii) the subsequent breeding density.

2. In the experiment, predation control effort was highly seasonal and designed to reduce partridge breeding season losses by killing resident predators of selected species.

3. The predation control significantly reduced the abundance of foxes, carrion crows and magpies during the critical partridge nesting period.

4. After the nesting period, predators re-established themselves each year, during late summer and early autumn.

5. The predation control significantly increased the proportion of partridges that bred successfully and the average size of their broods, thus substantially improving the production of young. Excluding effects of site and year predation control increased August numbers by 75%. Incorporating the effects on breeding stocks in subsequent years this led to an overall 3·5-fold difference between autumn populations with and without predation control.

6. Predation control significantly increased partridge breeding stocks the following year. Breeding stocks in years following predation control were 36% larger than stocks in years that did not follow predation control—excluding the effects of year and site. After 3 years this had produced a 2·6-fold difference in breeding density between the sites with and without predation control.

7. These results suggest that predators play a key role in limiting production and subsequent breeding density of partridges.

Key-words: experiment, gamekeeper, game management, grey partridge, nest predation, predator control.

Journal of Applied Ecology (1996) **33**, 965–978

Introduction

The grey partridge (*Perdix perdix* L.) is a widespread and economically important gamebird which has adapted to small-grain cereal farming. Following successful introductions into North America, the species had by 1930 a widespread Holarctic distribution. It was Europe's most numerous gamebird with over 20 million shot annually in the 1930s. Population declines resulted in a reduction in the bag to 3·8 million by the mid-1980s (Potts 1986) with further reductions since (Potts & Aebischer 1995). This population reduction has become an important conservation concern (Tucker & Heath 1994).

Southwood & Cross (1969) attributed the partridge decline to high chick mortality caused by reduced insect abundance following the introduction of herbicides in the 1950s. Potts (1973) and Potts & Vickerman (1974) confirmed strong associations between chick survival and insect abundance, but also identified predation as important. The key role of insects to chick survival was subsequently confirmed by radio-tracking broods (Green 1984; Rands 1985). Multi-site experiments with reduced herbicide use on field mar-

gins—Conservation Headlands (Rands 1985; Oliver-Bellasis & Sotherton 1986; Sotherton, Boatman & Rands 1989) proved the link between herbicide use and chick survival. Meanwhile, Potts (1980, 1986) in studies of partridges on the Sussex Downs, showed that predation on breeding birds was density-dependent in populations where there was no predator control by gamekeepers. When built into a simulation model this density-dependent effect suggested that predation could have a large effect on both autumn and spring stocks. This implied an effect of predation far greater than had been perceived by other gamebird ecologists on red grouse (*Lagopus lagopus* L.), e.g. Jenkins, Watson & Miller (1964).

This paper describes the results of a 6-year experiment designed to test the effect of predation during the breeding season, and the effectiveness of the predation control aspect of gamekeeping on abundance and breeding success of grey partridge.

Materials and methods

EXPERIMENTAL DESIGN

Our null hypothesis was that predators had no effect on the breeding success of grey partridges and so reducing numbers of predators would make no significant difference to breeding success, post-breeding partridge stocks or the subsequent breeding density.

The experimental design was to take two similar, but well separated study areas with similar partridge densities and manage one by reducing the rate of predation, while at the same time comparing the annual results with the other not subject to predation control. This was continued for a 3-year period (Phase I). The treatments were then reversed for the next 3 years (Phase II) with predation control at the second site and the formerly treated site left unmanaged.

It is important to note that the only treatment undertaken was a seasonal reduction in predator numbers, to reduce predation risk. There was no habitat management, winter feeding or modifications of the farming such as reduced pesticide use.

STUDY AREA

The two experimental study areas were located on Salisbury Plain, Wiltshire (1°45′ West, 51°15′ North). Both areas were on the Ministry of Defence training area of Salisbury Plain East, which was part of a block used for army exercises. The first area, Collingbourne (O.S. reference SU230520), measured 564 ha and was on the north-east edge near the village of Collingbourne Ducis. The second area, Milston (SU170470), measured 496 ha and was in the south-west corner, just north of the army town of Bulford. Six kilometres separated the two sites.

The ground was a rolling chalk upland (120 m) with thin, free-draining soils in most places. There were some small woods mostly of mixed beech (*Fagus sylvatica* L.), Scots pine (*Pinus sylvestris* L.) and elder (*Sambucus nigra* L.), as well as areas of scrub elder and hawthorn (*Crataegus monogyna* von Jacquin). There were a few scattered plantations of pine and poplar (*Populus* spp.). However, much of the area consisted of unimproved downland turf which was either left rough, grazed in sections by sheep and cattle, or cut for hay. The remaining land was rented to tenant farmers who grew principally arable crops (wheat, barley, oilseed rape, field bean and potatoes), as well as some grass, forage rape, and turnips for dairy cows and sheep (Fig. 1).

The land was administered by the Defence Land Agent and, theoretically, all of it could be used at any time for army exercises. In practice the land was graded so that most of the training activity took place on the grassland and little on the arable. The area was crossed by footpaths and military tracks, and although not formally open, the public always had access.

Rabbit (*Oryctolagus cuniculus* L.) numbers were reduced as and when necessary by farmers and land agent staff, as were woodpigeons (*Columba palumbus* L.) and rats (*Rattus norvegicus* Berkenhout). A gamekeeper was employed by the Bulford and Tidworth Garrison shoot which had the game shooting rights to 7280 ha including both study areas and he undertook some limited predator control on both study areas up to and including 1984. Afterwards, none was undertaken on or near the study sites except by us as part of the experiment. The nearest other predator control activity was some autumn fox shooting in areas south and south west of Tidworth to protect pheasant release pens (more than 3 km from the boundaries of either Milston or Collingbourne). Partridge shooting was continued at both sites throughout the experiment, but was restricted to 2 days only per site each autumn.

PREDATION CONTROL

Reductions in numbers of predators were carried out by one of us (Brockless) who is a professional gamekeeper. The principles which were used have a long history (Maxwell 1911; Middleton 1935; Anon 1994), but have evolved in response to increasing knowledge and environmental legislation. Our objective was to reduce predation losses, not to eliminate or exert a general population control on predators. Thus, predation on partridges is severe during their nesting period, but in most places is generally low through the rest of the year. Potts (1980), using data from six separate studies, calculated adult losses at 0·048 per month outside the breeding season, whereas losses up to 0·6 of all females were possible during incubation (Potts 1980). Consequently, removal of predators was seasonal and timed to coincide with partridge breeding which began in mid-April. However, other factors
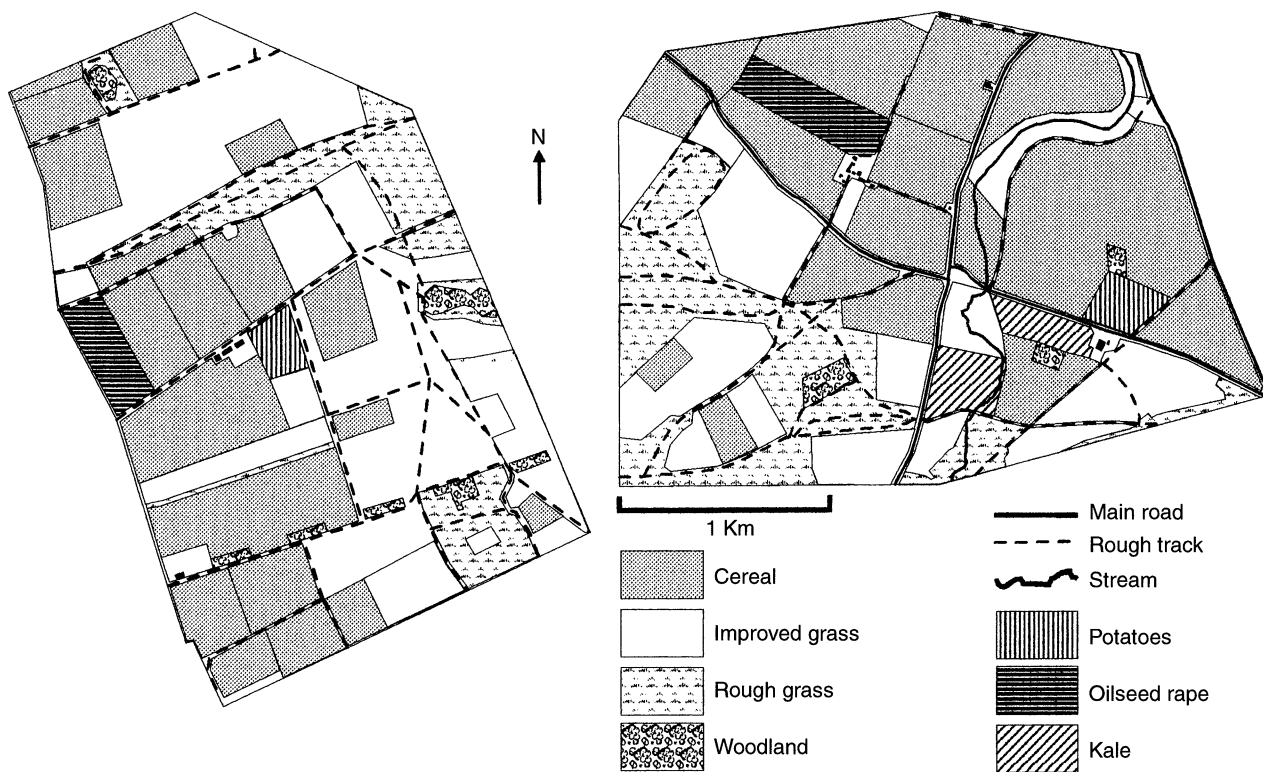
Fig. 1. Habitat on the two study sites Milston (left) and Collingbourne (right) in 1984. Collingbourne is 6 km north-east of Milston. Military training was largely confined to the grass, woodland areas and the trackways. Scale refers to both.

such as the seasonal behaviour of predators and their trappability was also taken into account. A strategy was worked out for each species or group of species, so that numbers could be reduced during the time when damage was likely to occur. There were three principal groups that were targeted for control.

Foxes (*Vulpes vulpes L.*)

Foxes kill adult hen partridges during incubation (Middleton 1935) and hen mortality is dependent on the density of breeding partridge pairs (Potts 1980). So, control of foxes was critical from the end of May and throughout June. The principal method employed against foxes was shooting with a rifle (a high-powered .222 calibre), both by day and at night with a spotlight. The open nature of the terrain on Salisbury Plain made this method particularly effective. Snares were also used occasionally to protect incubating hens in vulnerable sites.

Corvids

All species of corvid are egg predators, and the carrion crow (*Corvus corone* L.) and the magpie (*Pica pica* L.) actively look for nesting birds during the spring. Partridge nests are vulnerable during the latter half of April and throughout May. During this period we aimed to remove all territorial pairs of crows and magpies, and to reduce the large flocks of rooks

(*Corvus frugilegus* L.) and jackdaws (*Corvus monedula* L.) by ≈ 20%. For magpies and crows, control began at the end of March, allowing them to set up territories and to exclude the large flocks of non-territorial birds from the study sites. Corvids were either shot or captured in small cage traps (Larsens) using decoys (Anon 1994).

Small ground predators

Stoats (*Mustela erminea* L.) and rats both take partridge eggs, and can kill hen birds, so numbers of these species were reduced with a network of spring traps (Fenn Mark IV) sited in tunnels in suitable habitat on both study areas. Weasels (*Mustela nivalis* L.), which occasionally kill partridge chicks, and a few non-target hedgehogs (*Erinaceus europaeus* L.), which sometimes take partridge eggs, were also taken in these traps. These traps were set between March and July and inspected daily.

Other mammals and birds

Other mammals and birds did prey on partridges or take clutches. Feral cats can kill hen partridges and they were dealt with occasionally. Badgers (*Meles meles* L.) can find and dig out nests, and occasionally sparrowhawks (*Accipiter nisus* L.) will find and systematically deplete a covey of young birds. However, both of these species have full legal protection and

were left alone. In the event, damage by these two species was not severe, though it was recorded on both areas.

PREDATOR NUMBERS

The experiment depended on the ability of the game-keeper to reduce the numbers of predators on the experimental area during the 2-month breeding season. As a measure of his success, the relative numbers of foxes, magpies and carrion crows were assessed on different occasions.

For foxes, night-time lamping with a spotlight was used to give an index of fox abundance on the two areas during the spring/summer period. Both study areas were relatively open, and with spotlight and binoculars it was possible to see foxes at a range of over 500 m in suitable weather conditions. The two sites were visited after dark and a large part of the area was scanned continuously from a vehicle whilst driving a set route. The routes were 16·5 and 16·7 km on the two areas, which allowed $\approx$ 75% of Milston and 73% of Collingbourne to be scanned. These counts lasted about 2 h at each site and 42 were conducted between 2 May and 8 August 1986 during the first phase of the project, and 28 were conducted between 8 May and 20 June in 1990 during the second phase of the project. There were no counts in other years.

Seasonal changes in magpie and crow numbers were monitored on both areas in 1989 from 13 February to 5 June by counting the numbers seen during a set walk each week. In length the walks were 4·25 km (Milston) and 5 km (Collingbourne), and took between 70 and 80 min on each area. During the course of the walk every magpie and carrion crow seen was recorded. This meant that, typically, 78% of Milston and 66% of Collingbourne was scanned with binoculars. Counting crows was stopped a week earlier than for magpies because young rooks and young crows could not be separated.

In addition, in March 1989, prior to the start of the seasonal predator reduction, the numbers of magpie and carrion crow pairs that set up territories on both study areas was determined by nest finding, and watching their feeding and territorial behaviour.

PARTRIDGES

Techniques for censusing and monitoring populations of partridges are well known (Middleton 1935; Potts 1980, 1986). There are two main opportunities for counting partridges each year: in spring (March–April), when the population is paired prior to breeding; and in August (actually until mid-September), when family groups (coveys) can be counted post-breeding. However, spring pair counts can sometimes be unreliable in windy weather conditions when birds skulk in hedges or in rank grassy areas where they may

be difficult to see. Also, there is still some dispersal of individual pairs through early April until nesting sites become fixed (Potts 1986).

In August young and old birds can be distinguished, and male and female sex determined amongst the old birds. Because young birds remain with their parents, average brood size and the number of pairs producing a brood can be calculated. Also, because adult male survival is generally high (0·95 between April and August) and non-breeding cocks are rare, an August count of the adult males gives a good estimate of breeding pairs (Potts 1986).

Results from the spring counts indicated breeding stocks either the same or lower than the ones calculated from the number of old males present in August. Since there clearly could not have been negative mortality, the only explanations could have been that either birds were regularly moving onto both our study sites in summer, irrespective of any predator control, or birds were often missed in the spring counts. The latter seemed much the most likely. In the formal analysis that follows, the number of breeding pairs has been taken as the number of adult males counted in August. It will also be shown that our conclusions would have been the same if data from our spring counts had been used as a measure of breeding stock.

We made both a spring and an August count each year. In spring, each field or area of open grass was scanned with 10 × 50 binoculars and each partridge pair recorded on a map. Counts were made from a vehicle in the early morning and the whole area covered at least twice. In spring, in most cases, it was not possible to drive onto crops and arable areas had to be viewed from nearby tracks, further decreasing the reliability of spring counts.

August counts were carried out over several days during the period after harvest and no later than mid-September. Usually, two observers with binoculars in a four-wheel drive vehicle covered the areas field by field either in the early morning or late evening when birds were actively feeding. Stubble fields were driven across in narrow strips so as not to miss any coveys. The study areas were covered at least twice, and since birds were not marked, particular care was taken to ensure that they were not double counted.

Exact numbers of birds shot on the areas were counted at the end of shooting drives. One of us was always present throughout the shoot day.

The experimental design included two sites and 6 years. So for testing the results of the partridge counts, an analysis of variance model was used that included the effects of treatment (predation control), site and year. It was important to use population parameters that were independent, and raw counts of birds or simple densities thst reflect population changes over more than 1 year are clearly not independent. The measures of breeding success that were used were the proportion of pairs that produced a brood, the aver-

age brood size and, consequently, the number of young produced per pair. In addition, at least part of the breeding season loss that affects production is the mortality of hen birds. This can be the result of the hens being killed on the nest by foxes, or hens being killed by grass mowing when nesting in hay or silage meadows. Consequently, populations subject to these pressures have fewer surviving adult females after breeding than other populations.

The number of broods produced in relation to the number of breeding pairs reflects not only this hen loss, but also those pairs that fail to hatch a clutch. This is most often caused by egg predators such as carrion crows.

The average brood size is primarily a reflection of how well the chicks survive after hatching and this will be affected by insect abundance (partridge chick food) and weather conditions—warm dry weather favouring chick survival and insect abundance. However, partridge pairs which lose clutches may subsequently lay second or third clutches that are smaller than the average first clutch. The effect of this is to produce only a small, often late hatched, brood.

Autumn and breeding stocks are best tested as changes from year to year, so for each year proportional changes (N_i/N_{i-1} for autumn stocks and N_{i-1}/N_i for breeding stocks) were calculated. It should be noted that in the analysis of change in autumn stocks there is arguably a difference where N_i and N_{i-1} are both treatment years, and where in N_{i-1} has a different treatment than N_i, i.e. the cross-over years. Therefore, another analysis of variance was performed with these cross-over years as an additional category to test whether cross-over years added significantly to the variation.

All analyses of variance were carried out on untransformed data as the residuals showed evident normality.

Results

THE PREDATORS

The seasonal nature of the predation control meant that most predators were killed in spring or early summer at a time when they were usually territorial. The consequence of removing a territorial corvid or carnivore is that neighbouring territory holders expand their territory to include the vacated area, and that animals without territories, and formerly excluded by the residents, move in and attempt to breed (Reynolds, Goddard & Brockless 1993). It is, therefore, essential to remove the replacements for the territorial animals until partridge breeding has been completed in July. After July the replacements can be allowed to re-establish themselves in the area, although for the corvids their territorial phase is largely over by this time. Thus, between late summer and April the following year, one would expect there to

be little difference in predator density between the experimental and control areas. Even during the critical months of April, May and June one would not anticipate that the experimental area would be devoid of predators as neighbours and immigrants appear before being removed.

This seasonal effort was evident from an analysis of annual numbers killed (Fig. 2), which shows the pronounced increases in numbers taken not only prior to but during the critical period.

It was not possible to determine the numbers of predators present on the experimental area during the partridge breeding season because most of the
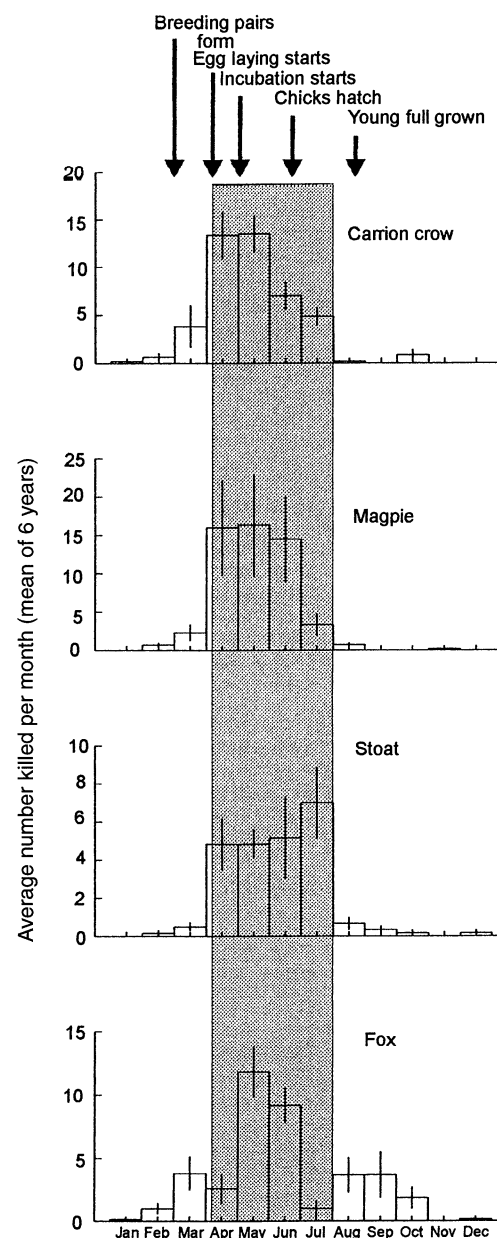

Fig. 2. Numbers of four species of predator killed per month throughout the experiment. Bars are means of 6 years with standard errors. Numbers show how control was timed to coincide with the main partridge breeding period—shaded and indicated at top.

Table 1. Number of sightings of adult foxes during summer spotlight surveys of the two study areas during the two experimental phases of the project. There were significantly fewer sightings seen at Collingbourne than at Milston during Phase I ($t = 2.625$, d.f. 40, $P = 0.006$ one-tailed) and there were significantly fewer sightings at Milston than at Collingbourne during Phase II ($t = 5.821$, d.f. 26, $P < 0.000$ one-tailed)

Study area	Fox sightings	Nights lamping	Sights per night	SE
Phase I (Summer 1986)				
Milston	30	20	1·5	0·21
Collingbourne*	18	22	0·82	0·16
Phase II (Summer 1990)				
Milston*	5	14	0·36	0·17
Collingbourne	96	14	6·86	1·10

*Predation control in effect.

residents were removed and the frequency at which they were encountered has to be taken as a guide. Table 1 shows the results of the two spotlight surveys of foxes that were carried out in 1986 during the first phase of the project and in 1990 during the second phase. This shows that significantly lower numbers of fox sightings were recorded on the areas with predation control irrespective of site. In addition, there was at least one litter of fox cubs on Milston in 1986 and at least two litters on Collingbourne in 1990 during the periods of no predation control, indicating not only resident, but breeding animals. Table 2 illustrates that the seasonal predation control significantly reduced the numbers of crows and magpies seen after 1 April. At Collingbourne there were six pairs of resident carrion crows and five pairs of magpies in spring 1989. At Milston there were also six pairs of carrion crows, but eight pairs of magpies in spring 1989 before control.

PARTRIDGES

During the course of the experiment, the two populations showed periods of growth and decline (Fig. 3).

The results of the August partridge counts are shown as the distribution of broods and associated old birds year by year (Figs 4, 5 and 6), and the main population totals are given in Table 3.

1984 was a good breeding season for partridges and, combined with some limited predator control by farmers and a local gamekeeper in that year, medium-sized and some large broods were found evenly distributed on both sites. In 1985, the first experimental year of Phase I, the weather conditions were poor, and breeding success was poor and uneven. High predation was evident at Milston with large numbers of old birds being seen, especially single males. At Collingbourne, production was good in the south-west corner, but elsewhere hen and nest losses still occurred. 1986 produced some fine weather and some large broods were found throughout the Collingbourne site, whereas at Milston there were only a few scattered broods and the large number of single male birds indicated heavy hen predation. 1987 was a cold wet summer and, even at Collingbourne, average brood sizes were down; at Milston production reached a minimum. In 1988, the beginning of Phase II, predation control was switched to Milston and heavy predation was evident at Collingbourne indicating a rapid return to unmanaged conditions, whereas at Milston production doubled, in spite of rather mixed weather conditions. 1989 showed continuing deterioration in production at Collingbourne and a further improvement in production at Milston. 1990 was the final experimental year and was characterized by ideal summer weather, and brood sizes were above average. The effects of predation control at Milston resulted in the highest autumn density of the 6-year experiment.

The effect of treatment (predation control) significantly increased the female/male ratio, all measures of breeding success, the autumn stock and the number of breeding pairs the following year (Table 4). In the analysis of changes in autumn stock, where the cross-over years were included as a separate category, there was no significant added variation due to

Table 2. Numbers of magpies and carrion crows seen in weekly surveys on the two study sites in spring 1989. There were significantly fewer magpies seen at Milston after 1 April than before ($t = 2.594$, d.f. 14, $P = 0.01$ one- tailed), as there were fewer carrion crows ($t = 3.26$, d.f. 13, $P = 0.003$ one-tailed). There was no significant difference in magpie or crow numbers before and after 1 April at Collingbourne

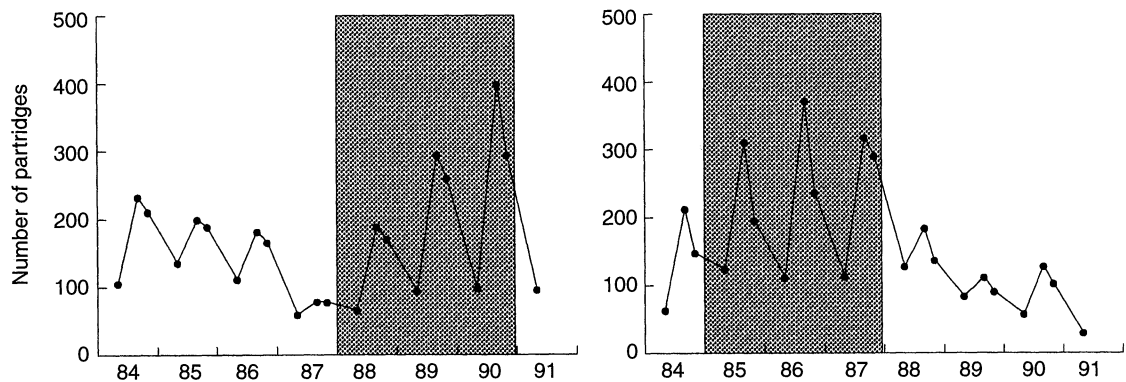| Study area	February	March	April	May	Birds per survey before 1 April	SE	Birds per survey after 1 April	SE
Magpies								
Milston*	10	20	7	4	4·29	1·08	1·33	0·55
Collingbourne	5	12	15	19	2·86	0·99	4·22	0·57
Surveys	3	4	4	5				
Crows								
Milston*	24	50	20	20	10·57	1·43	5·00	1·00
Collingbourne	41	82	38	72	17·57	2·81	13·75	2·08
Surveys	3	4	4	4				

*Predation control in effect.

Fig. 3. Yearly and seasonal changes in the population of partridges at Milston (left) and at Collingbourne (right). Data points are for spring stock, autumn stock and post-shooting stock. Except for the 1991 spring count all numbers are calculated from August counts and known numbers killed on shooting days.

this separation. So in the analyses in Table 4, cross-over years and other years are treated as the same. After removing the effects of site and year, predation control was estimated to improve autumn stock by 75% annually (the estimated change in year-on-year ratio attributable to predation control was 0·75 from the analysis of variance model) and breeding pairs by 36% annually (calculated in the same way). The effects on autumn stock and breeding pairs were, to some extent, cumulative, so that during each experimental 3-year phase the two populations diverged. Using Table 3, in August 1987, the Collingbourne autumn density was 3·53 times Milston's and by spring 1988 the density of breeding pairs was 1·7 times that of Milston's. At the end of the second phase, autumn stock at Milston was 3·54 times that of Collingbourne and the subsequent spring density was 3·63 times greater. Taking the average of these two phases,

autumn stock during the predation control phases reached 3·5 times and spring stock reached 2·6 times the untreated population.

In Table 4 there was significant added variation due to year in those measures that contain a large element of chick survival (brood size and number of young per pair). These were consistent with the known effects of chick food supply and weather on chick survival. The two significant added variations due to site were most likely due to the way the grassland was managed on the two areas. At Milston more of the managed grassland was mowed for hay and silage than at Collingbourne and this grass cutting explains the higher female mortality (female/male ratio = 0·69 at Milston and 0·78 at Collingbourne, excluding the effects of treatment and year). However, at Collingbourne, much of the grass was used for sheep grazing and this could have resulted in disturbance and subsequent
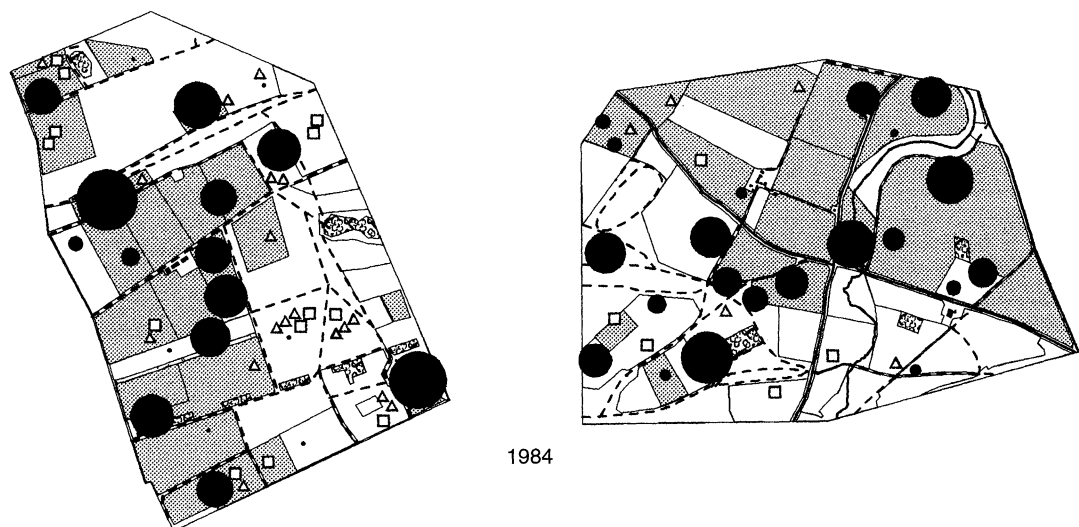
1984

Fig. 4. August counts of partridge on Milston (left) and Collingbourne (right) in 1984 prior to the start of the experiment. Cereal fields are shaded; most of the rest of the area is grassland (see Fig. 1). The location of broods (a cock and a hen bird with a variable number of young chicks) are shown as variable sized black discs; the number of young birds is proportional to the diameter of the disc ranging from one young to 18 which occurred twice—at Collingbourne in 1985 and Milston in 1989. Open squares indicate unsuccessful pairs of partridges with no young (caused principally by nest or egg losses) and triangles indicate single male birds (caused by the loss of the hen). Symbols are plotted where birds were first seen, but some are shifted slightly to show all data.
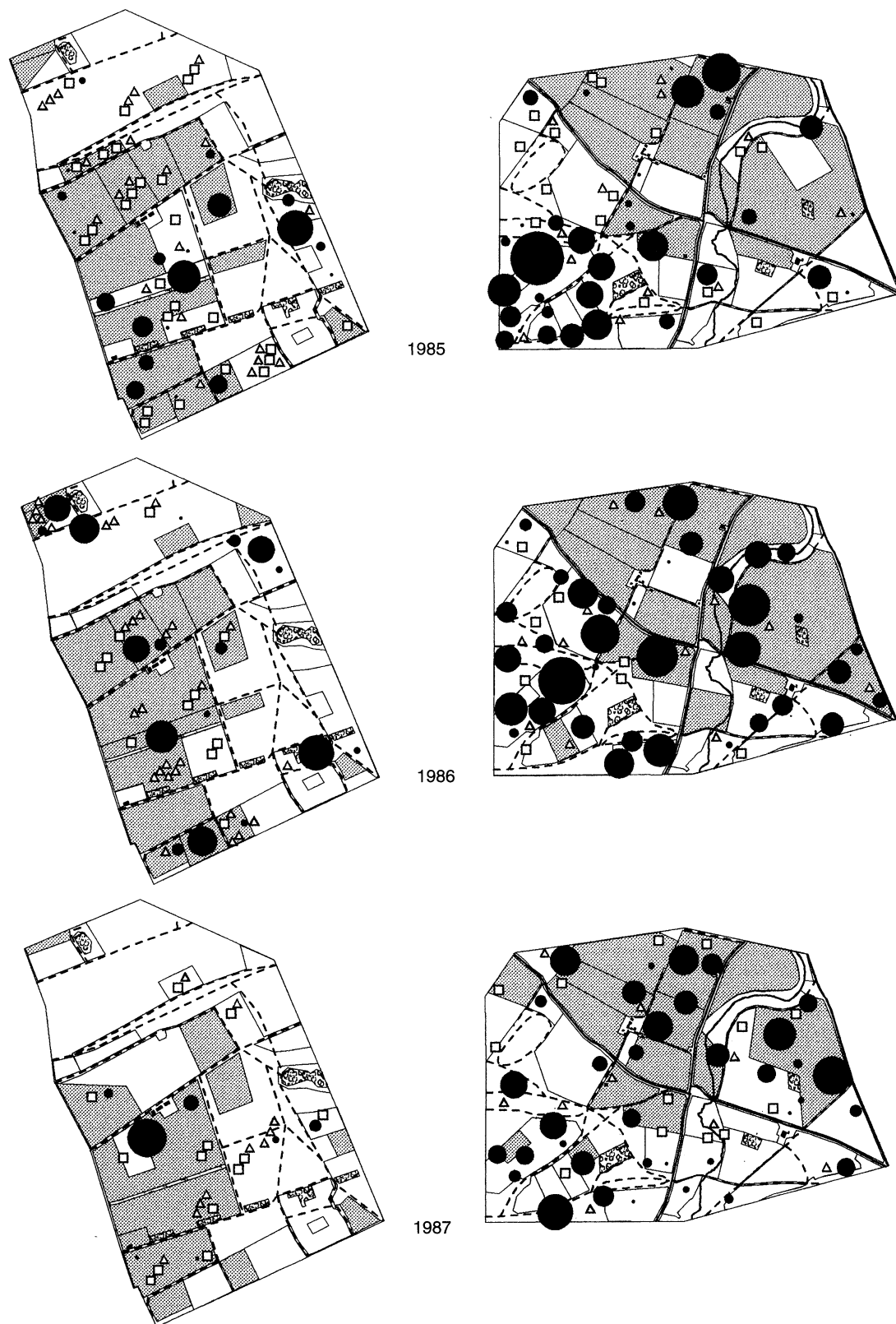
Fig. 5. Partridge counts for Phase 1. Collingbourne area (right-hand side) with predation control. Symbols as for Fig. 3.

losses of more nests than at Milston (broods per pair = 0·66 at Milston and 0·57 at Collingbourne, excluding the effects of treatment and year).

It has been shown that winter losses in partridges are often density-dependent (Potts 1980, 1986), so

year-to-year changes in breeding stock may also be partially related to breeding density itself. To check this, the analysis of variance of changes in breeding stock were repeated, but including the density (year i of the years i and $i + 1$) as a covariate. The effect of

S.C. Tapper,
G.R. Potts &
M.H. Brockless
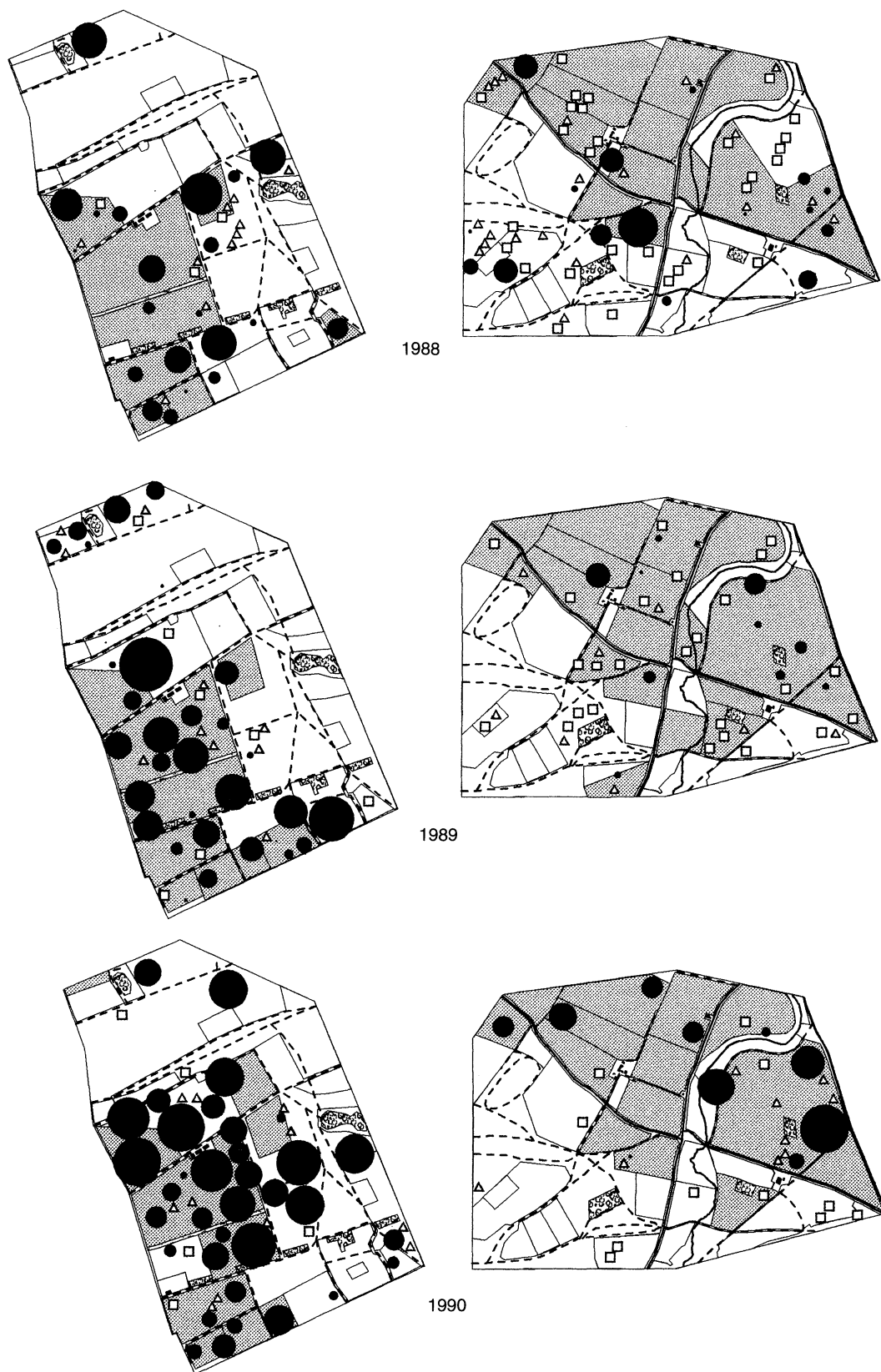
Fig. 6. Partridge counts for Phase 2. Milston area (left-hand side) with predation control. Symbols as for Fig. 3.

breeding density was not significant, nor did it alter the significance of the other factors.

The data from our spring counts showed the same effect as those derived from August counts—in years

following summers of predation control spring densities increased in five cases out of six, and in years following no summer predation control, the densities declined in five cases out of six. Breeding stocks cal-

Table 3. Annual partridge stocks and reproductive success from 1984 to 1991. Predation control in operation between 1985 and 1987 at Collingbourne (Phase 1) and between 1988 and 1990 at Milston (Phase 2). (a) Counts of birds made in August or numbers recorded shot in September. (b) Derived measures of reproductive success and density, all based on August counts except 1991 spring density which was based on a spring count

(a)

Year	Adult males	Adult females	Juveniles	Broods	Total birds	Number shot
Collingbourne						
1984	32	24	157	21	213	65
1985*	62	50	199	34	311	116
1986*	56	42	274	37	372	135
1987*	57	50	211	37	318	27
1988	64	44	76	16	184	47
1989	42	35	35	10	112	21
1990	29	21	78	10	128	25
Milston						
1984	53	32	148	19	233	22
1985	68	46	86	20	200	11
1986	56	28	98	17	182	16
1987	30	20	29	7	79	1
1988*	33	23	133	21	189	19
1989*	47	37	211	30	295	35
1990*	49	40	310	35	399	105

(b)

Year	Mean brood size	Young per pair	Birds km^{-2} August	Pairs km^{-2} Spring
Collingbourne				
1984	7·48	4·91	37·77	5·67
1985*	5·85	3·21	55·14	10·99
1986*	7·41	4·89	65·96	9·93
1987*	5·70	3·70	56·38	10·10
1988	4·75	1·19	32·62	11·35
1989	3·50	0·83	19·86	7·44
1990	7·80	2·69	22·70	5·14
1991				2·66
Milston				
1984	7·79	2·79	46·98	10·68
1985	4·30	1·26	40·32	13·71
1986	5·76	1·75	36·69	11·29
1987	4·14	0·97	15·93	6·05
1988*	6·33	4·03	38·10	6·65
1989*	7·03	4·49	59·48	9·47
1990*	8·86	6·33	80·44	9·88
1991				9·67

*Predation control in effect.

culated from spring counts had 24 fewer birds, on average, than when they were calculated from August counts.

The effect of predation control on breeding stock was further checked by repeating the analysis of change in breeding pairs using the counts of pairs made in spring. This produced a similar outcome to the analysis based on counts of adult males in August. There was no effect of year or site, but the effect of treatment (predation control) was significant ($P = 0.027$). After adjusting for effects of site and year, the estimated effect of predation control was to increase the numbers of spring pairs by 42% annually.

The consequences of variation in autumn stock were threefold. First, it altered the proportion of birds shot (Fig. 7a). This resulted mainly from hunters deliberately reducing effort in poor breeding years in order to conserve stocks for next spring—as is usual. Secondly, the loss of birds overwinter tended to increase with density (Fig. 7b). Although these data were not statistically significant, overwinter loss has been shown elsewhere to be density-dependent and related to suitable nesting habitat (Potts 1980, 1986). Thirdly, the number of birds left after shooting was positively related to the breeding stock the following year (Fig. 7c). So with this regime of shooting, not only

Table 4. Results of analysis of variance of measures of partridge breeding success and population change on both study sites between 1985 and 1990 inclusive

| Source of variation	Sum of squares	d.f.	Mean square	F ratio	P
Female/male ratio					
Treatment—predation	0·036	1	0·036	16·563	0·0152*
Site	0·022	1	0·022	10·281	0·0327*
Year	0·045	5	0·009	4·058	0·1
Error	0·009	4	0·002		
Broods per pair					
Treatment—predation	0·472	1	0·472	156·909	0·0002***
Site	0·026	1	0·026	8·687	0·0421*
Year	0·068	5	0·014	4·545	0·0838
Error	0·012	4	0·004		
Mean brood size					
Treatment—predation	9·955	1	9·955	23·443	0·0084**
Site	0·166	1	0·166	0·390	0·5661
Year	17·063	5	3·413	8·036	0·0327*
Error	1·699	4	0·425		
Mean young per breeding pair					
Treatment—predation	26·859	1	26·859	183·371	0·0002***
Site	0·449	1	0·449	3·065	0·1549
Year	7·288	5	1·458	9·951	0·0224*
Error	0·586	4	0·146		
Change in autumn stock					
Treatment—predation	1·687	1	1·687	11·506	0·0275*
Site	0·241	1	0·241	1·642	0·2693
Year	0·787	5	0·157	1·074	0·4860
Error	0·586	4	0·147		
Change in breeding pairs					
Treatment—predation	0·385	1	0·385	14·324	0·0194*
Site	0·082	1	0·082	3·037	0·1563
Year	0·207	5	0·041	1·538	0·3487
Error	0·108	4	0·027		

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$.
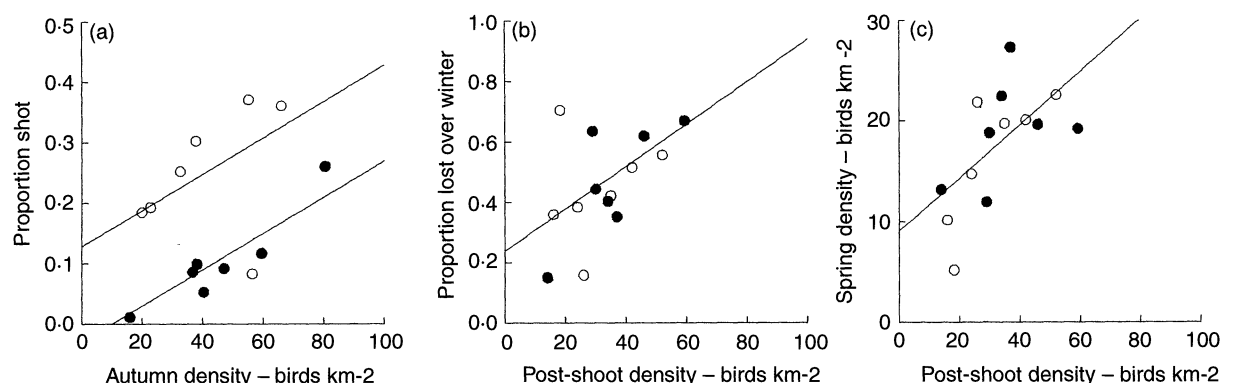
Fig. 7. Partridges; spring 1984 to spring 1991. The effect of autumn density on subsequent population changes. Open circles are for Collingbourne and filled circles are for Milston. (a) The increasing proportions shot in relation to autumn density. Data for the two sites were significantly different ($P = 0.002$), but there was a significant trend through the combined data ($P = 0.025$). (b) The proportion lost over winter after shooting in relation to numbers left after shooting ($P = 0.076$). There was no significant difference between the sites. Right (c) shows the relationship between autumn density after shooting and breeding density the following spring ($P = 0.027$). There was no significant difference between sites. [Note that in (a) and (b) the Y variable is partially dependent on the X variable. However, the effect of this dependence would be negative not positive and so does not invalidate our conclusions]. Analysis of covariance used throughout.

were higher game bags achieved following summers of predation control, but breeding stocks were increased or maintained a higher level as well.

Discussion

This experiment has shown that a seasonal reduction in the number of predators significantly and substantially improves the breeding success of partridges, resulting in not only higher August stocks, sufficient to sustain some shooting, but significantly improves the breeding density as well. This was brought about by more pairs breeding successfully and producing larger broods. The periods without predation control were characterized by small summer increases due to poor breeding success, very small and, therefore, almost inconsequential shooting bags, and over-winter losses which tended to reduce as the breeding population declined. The periods of predation control showed large summer increases, normally larger shooting bags and a breeding stock which was stable or increasing.

In the past, landowners and gamekeepers relied on predator control to produce a shootable surplus and to increase breeding stocks of red grouse, pheasant (*Phasianus colchicus* L.) and red-legged partridge (*Alectoris rufa* L.), as well as grey partridge (Tapper 1992). However, most early gamebird research concentrated on other factors which limited populations on well managed estates. This was because predator control was always considered an essential ingredient in game management (Lovat 1911; Middleton 1935).

In the post-war era, population studies focused on the regulation of breeding densities of birds, both in species which had relatively stable spring numbers (grey partridge) and others where these densities fluctuated widely (red grouse). For grey partridge, winter losses in relation to habitat quality were considered the primary factor limiting spring numbers and winter habitat improvement was seen as the most important management priority (Jenkins 1961). However, after the introduction of herbicides into cereal farming chick mortality increased and appeared to be the key factor in causing variation in breeding success (Blank, Southwood & Cross 1967). These authors also claimed that chick mortality was density-dependent and could be a density-regulating factor as well. However, this finding was caused by their population suffering increasing rates of chick mortality due to the introduction of herbicides, at the same time as showing a progressive increase in density due to predation control. Nevertheless, they continued to believe that habitat was the main factor regulating breeding density (Southwood & Cross 1969). In red grouse, a succession of studies based at Banchory emphasized, in turn, the role of habitat, nutrition, behaviour and genetics as being the main forces regulating spring densities of these birds (see Moss & Watson 1980; Watson & Moss 1980). These studies were highly

influential and became incorporated into standard texts (e.g. Ricklefs 1973), although more recently, Bergerud (1988) has questioned the work and drawn attention to the importance of nest predation.

The near absence of serious studies of the role of predation on either breeding densities or breeding success seems to have three causes. First, populations of many predators were much lower two decades ago than today, particularly raptors, corvids and some carnivores (Sharrock 1976; Arnold 1978, 1993; Newton 1979; Tapper 1992; Gibbons, Reid & Chapman 1993; Morris 1993). Secondly, some authors misinterpreted what gamekeepers were doing, believing that because they trapped similar numbers of predators each year they were merely removing a doomed surplus in the same way as the game itself was cropped (e.g. Jenkins, Watson & Miller 1963; Tapper, Green & Rands 1982). Thirdly, most of the key studies on gamebirds were actually being done on areas where predators were controlled by gamekeepers, so the effect of predation was not as severe as it might otherwise have been. This was true for the partridge studies at Micheldever (Jenkins 1961), at Damerham (Blank *et al.* 1967) and at Sutton Scotney (Blank *et al.* 1967; Southwood & Cross 1969). Only later, on the South Downs, were areas with and without gamekeepers compared (Potts & Vickerman 1974; Potts 1980). Predators were also controlled on the main red grouse study areas at Glen Esk and six other subsidiary sites (Jenkins *et al.* 1963).

Newton (1993) has recently reviewed the role of predation in bird populations and concluded that, although mortality due to predation was unlikely to be always compensatory, many bird populations have reservoirs of non-breeders which can replace losses to predators. He concluded that two groups of birds, waterfowl and gamebirds, appear to be particularly prone to predation, but only in woodpigeon (Tomialojc 1980), black grouse (*Tetrao tetrix* L.) and capercaillie (*Tetrao urogallus* L.) (Marcström, Kenward & Engren 1988), ruffed grouse (*Bonasa umbellus* L.) (Keith & Rusch 1988) and in grey partridge (this study) have experiments been carried out that demonstrate that improved production results in improved breeding stock.

It is tempting to regard predation control as simply a means to produce abnormally large autumn numbers of gamebirds for sport shooting, and that it has little or no conservation merit because the effects on spring densities are slight and are outweighed by the negative effects on the status of predators. Certainly, the main purpose has always been to produce birds for shooting and it is usually argued that the main conservation benefits are the associated habitat management practices. However, this experiment shows that even within a 3-year period the difference between sites with and without predation control can amount to a 2·6-fold difference in spring densities. It is not clear whether this difference would increase or sta-

bilize with time, although Potts (1986) calculated that equilibrium levels would be achieved in 6–7 years.

Although agricultural intensification remains a major problem, it is certain that breeding stocks of grey partridge continue to decline all over Europe (Tucker & Heath 1994). In Britain this has led to local extinctions and an 18·7% reduction in breeding range during the last two decades (Gibbons *et al.* 1993). In view of this situation, predation control should be viewed a proven and effective conservation tool in the same way as habitat management and reduced pesticide use.

Acknowledgements

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