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The distribution and abundance of the Rook *Corvus frugilegus* L. as influenced by habitat suitability and competitive interactions.

Thesis submitted in accordance with the requirements of the University of Durham for the degree of Doctor of Philosophy

By

Larry Roy Griffin

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October 1998

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Abstract

Rooks (*Corvus frugilegus*) are colonially breeding corvids found in most agricultural landscapes. Colonies in the County Durham area tend to be clustered at distances up to 500 m, but otherwise show little pattern in terms of spacing or size. Colony size was comparable between sites as changes in colony nest counts were allowed to stabilise before the whole area was surveyed. When measuring nest build-up at a sample of colonies in 1996, no further significant increases occurred after 9th April. The spatial size distribution of colonies was maintained between years.

The distribution and size of breeding colonies is modelled in relation to the interaction between the spatial distribution of the foraging habitat and potential intraspecific competitors, with the identification of the distance over which this interaction is strongest. The satellite derived habitat data used for the modelling were part of the ITE Land Cover Map of Great Britain. However, their correspondence with ground reference data was found to be severely lacking. Thus, for modelling the availability of nesting habitat, OS woodland data were used as these identified more of the extant rookery sites, whilst the ITE data were retained for quantifying the foraging habitat.

Logistic regression showed that the distribution of colony sites was influenced by the availability of woodland blocks large enough to hold a colony, proximity to roads and buildings, and by the amount of pasture within 1 km. Other suitable sites with these characteristics remained unoccupied within the distribution.

Partial Correlations showed that interactions between the spatial distribution of the foraging habitat and competitors influenced colony size at distances up to 6 km, suggesting their effect outside of the breeding season. The multiple regression model built with variable values for this distance explained 31% of the variance in colony size. When applied to the potential breeding sites identified using the logistic regression, most sites still remained suitable. This suggests the distribution is not saturated and that limited availability of breeding habitat is not the cause of the nesting aggregations.

The broad correlation of Rook abundance to foraging habitat and potential competitors corresponds to an ideal free distribution of individuals across colony sites. This is supported by models of Rook numbers in relation to parish agricultural statistics produced by MAFF. These again show the importance of pasture as a probable foraging resource, and how pasture quality could be important to Rook numbers. The models also supported the ideal free predictions of spatial variation in Rook abundance in relation to habitat, and the response of colony sizes to temporal change in habitat quality.

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Thanks also go to Chris for allowing me to try and investigate Rooks from other angles. This included a Rook trap which was stolen, and tree climbing efforts which never quite got off the ground because either the ladder was cunningly crafted from concrete or the trees had grown since I saw them last.

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This thesis is dedicated to the loving memory of my dad, Kenneth Edward Griffin.

Chapter 1

1 General introduction

1.1 Layout of the thesis

- In Chapter 1, I will review theories on the evolution of coloniality in birds. Studies of the variation in colony size have led to the most recent hypotheses of the evolution of coloniality. The current study aims to investigate the specific relationship of colony size in the Rook *Corvus frugilegus* L. to habitat structure and intraspecific competition. The Rook was chosen as a study species because colonies are relatively easy to find and count, and because information on its well-defined foraging and nesting habitat is available over large areas. The multivariate models developed in this thesis using the capabilities of Geographical Information Systems (GIS) will be used to investigate some of the predictions arising from the various theories on the evolution of coloniality, outlined in Chapter 1. The use of a GIS will enable the definition of the rookery sampling unit to be changed in accordance with the aims of each chapter.
- In Chapter 2, the Rook colony dataset is described along with the methods developed for data collection. The data are analysed for spatial patterns in terms of the distribution of colonies and changes in their size.
- In Chapter 3, the satellite-derived habitat map produced by the Institute of Terrestrial Ecology (ITE), and used for future modelling in this thesis, is described and compared with ground reference data and aerial photo interpretation data collected for a test area within County Durham. The ability of the habitat map to depict field types used for foraging by Rooks, and the woodland blocks used for nesting, will be assessed.

- In Chapter 4, the ability of the ITE data, compared to the Ordnance Survey (OS) data, to depict rookery woods will be assessed. The OS data will also be used to build a model of habitat selection by Rooks, in relation to various landscape features determined from both the ITE and OS data.
- In Chapter 5, the relationship of Rook colony size to available foraging habitat and potential intraspecific competitors in areas of increasing radii around focal colonies will be modelled to assess the likely distance over which Rooks forage and the field types most often utilised. The resulting model will be used to predict colony size for the woodlands identified as being potentially suitable for colonisation in Chapter 4.
- In Chapter 6, the relation of Rook numbers to any of the ITE land use types identified in Chapter 5 will be verified using an independent source of data on the agricultural land use types in the study area produced by the Ministry of Agriculture, Fisheries and Food (MAFF). The MAFF data will also be used to test for a relationship between colony size and livestock variables which may affect the forage quality of pastures, and to test for habitat variables which are linked with changes in Rook numbers through time.
- In Chapter 7, the conclusions of this thesis will be highlighted and discussed in relation to the limitations of the methodologies and habitat data used, and in relation to the evolutionary theories outlined in chapter 1.

1.2 Introduction

This chapter will outline theories on the evolution of coloniality and variation in colony size, and how they relate to the Rook *Corvus frugilegus* L., in particular. Also GIS terminology and procedures used throughout this thesis will be highlighted.

Due to the vast literature available on the sociality of animals in general, this introduction will be limited to examples relating to bird species. However, many of the concepts developed in this field took inspiration from, or have inspired, research in other animal groups.

Species exhibit varying tendencies towards aggregation when feeding, breeding or roosting and one or more of these aggregation types may be characteristic of a species. Explanations have either focused on the unique selection pressures acting in each situation, or have attempted to explain the parallels in spacing behaviour in terms of some common factor. Therefore, the introduction includes examples relating to communal roosting alongside those dealing with colonial breeding aggregations where similar principles are thought to apply.

1.3 Definition of coloniality

The definition of a colonial species is problematic as there is probably a continuum from solitary (territorial) through semi-colonial to colonial nesters (Coulson & Dixon 1979). The term "coloniality" is used here to refer to individuals that are clumped in space more than expected on the basis of resource patchiness (Brown & Orians 1970), or that are "breeding among densely distributed territories that contain no resource other than nest sites" (Danchin & Wagner 1997). Even with these definitions, defining a colony unit can still prove problematic (Coulson & Dixon 1979). In Rooks, for example, the definition of a colony is often based on subjective impressions of nest groupings (Nicholson & Nicholson 1930; Wynne 1932), which have been standardised to the 100 m separation distance used for survey purposes (Sage & Nau 1963; Patterson *et al.* 1971; Sage & Vernon 1978; Sage & Whittington 1985; Brenchley 1986). Alternatively, the definition may be based on observed behavioural interaction between members of different nesting groups (Coombs 1961a).

1.4 Evolution of coloniality

It is assumed that coloniality is favoured over a solitary existence only if the fitness pay-offs for individuals are higher in aggregations. However, there are two automatic detriments to breeding in a colony: increased competition for resources (e.g. nest sites, mates and food); and increased likelihood of parasite and disease transmission (Alexander 1974; Hoogland & Sherman 1976; Coulson & Dixon 1979). Also, group living may increase the chances of: being detected by a predator; losing offspring to intraspecific killing; or raising genetically unrelated young (Hoogland & Sherman 1976). Balancing these negative factors which would act to disperse organisms, eight hypotheses advocating the benefits of coloniality have been proposed.

1.4.1 Nest-site-limitation hypothesis

Lack (1968) suggested that coloniality evolved due to limitation in the number of safe sites for nesting. Where this resource was clumped, as on oceanic islands, so the nesting distribution became clumped in response. In the Swallow *Hirundo rustica*, nest numbers increase in parallel to the increase in barn size used, implying colonies are site limited, passive aggregations (Snapp 1976).

Møller (1987) however, disagreed with this finding and suggested that Swallows tend to aggregate actively at specific sites. The correlation with barn size would be expected because only a certain number of nests can be fitted into a finite area. In reviewing the literature for seabirds, Clode (1993) agreed that even in highly aggregated species, nest sites are often not limiting. This was also found to be the case for Bearded Tits *Panurus biarmicus* (Hoi & Hoi-Leitner 1997), Fieldfares *Turdus pilaris* (Wiklund & Andersson 1994) and Great Blue Herons *Ardea herodias*, whose highly variable nest and colony characteristics led Gibbs *et al.* (1987) to conclude that suitable habitat did not limit colony size or distribution. Among seabirds, there is likely to be variation in the factors limiting colony size, and there is evidence that in Sooty Terns *Sterna fuscata*, for example, colonies are limited by the space available for nesting (Feare 1976). For the Rook in particular, nest sites do not appear to limit the size or spatial distribution of colonies to any great extent (Murtland 1971; Patterson *et al.* 1971).

Therefore, it seems likely that safe nest sites are only limiting in special circumstances and are unlikely to have led to the evolution of coloniality in most species. The use of the term "safe", obviously implies the influence of aerial and/or ground-based predators upon the evolution of coloniality, and so this hypothesis overlaps with those concerned purely with predation.

1.4.2 Predation hypotheses

Although an integral part of the nest-site-limitation hypothesis, predation pressures may have given rise to coloniality independently. Individuals in groups can benefit from "selfish herd" or dilution effects and predator swamping (Hamilton 1971), early detection of predators and reduced vigilance times (Pulliam 1973; Hoogland & Sherman 1976) and/or social mobbing (Robinson

1985; Wiklund & Andersson 1980). However, studies into the effects of increased clumping on nest predation have shown negative trends (Hoogland & Sherman 1976; Hagan III & Walters 1990; Wiklund & Andersson 1980; Wiklund & Andersson 1994; Anderson & Hodum 1993), positive trends (Lemmetyinen 1971; Burger 1974; Pienkowski & Evans 1982) or no trend at all (Snapp 1976; Møller 1987; Hoi & Hoi-Leitner 1997), such that its influence on breeding dispersion is far from clear (Anderson & Hodum 1993; Danchin & Wagner 1997).

The link between predation and the evolution of communal living is also disputed by observations of communal breeding and roosting in large raptor species which are unlikely to be predated upon (Ward & Zahavi 1973). Similarly, Clode (1993) noted that the densest seabird colonies are often on off-shore islands and sea cliffs in areas free from ground-based predators, while those exposed to aerial and ground-based predators are ground nesters that often live solitarily or in small colonies on the mainland. This comparative evidence suggests that coloniality is not a response to predation and that the anti-predator behaviours seen at colonies or roosts are in fact a response to increased predation pressures (Zahavi 1971; Rodgers 1987). Ward & Zahavi (1973) considered that the spectacular aerial displays at colonies or roosts would actually advertise the location to predators, so that these assemblages cannot have evolved for predator avoidance.

However, these arguments are based on species whose predators may be more or less abundant than they were only a century ago, thus weakening the evolutionary inferences that can be drawn from studies of present-day behaviour (Anderson & Hodum 1993). In an undisturbed predator-prey system (Galápagos Hawks *Buteo galapagoensis* on the Blue-footed Booby *Sula nebouxii*), it was found that chicks in isolated nests were taken out of proportion to their availability at the time of each predation event (Anderson & Hodum 1993). Although this suggests clumping was beneficial, the study was based on nest dispersions which varied continuously, rather than on truly solitary versus colonial breeders.

On balance, the evidence points to density-dependent predation rates as being an attribute of coloniality rather than a cause.

1.4.3 Central-place-foraging/Horn's geometric model

Brown (1964) suggested that territoriality was related to the economic defendability of a uniformly dispersed food supply. Horn (1968) proposed that temporal and spatial uncertainty in the position of food supplies would result in nest clumping, because the patches become undefendable and best exploited from a central location. With clumping, mean flight distances for average colony members become less than those for average members of a dispersed population. This remains so for colonies displaced by up to 70% of the radius from the centre of a circular foraging range (Wittenburger & Dollinger 1984). However, the central placement of colonies within circular feeding areas, with the minimisation of travel distances to food patches, would be expected even if colonies evolved for other reasons (Covich 1976).

Brown *et al.* (1992) noted that, because the model's critical assumptions of an externally bounded feeding area and a uniform distribution of potential nest sites probably seldom hold for natural populations, Horn's model is unlikely to explain the evolution of coloniality. Brown *et al.* (1992) showed that the observed travel distances of Cliff Swallows *Hirundo pyrrhonota* were on average 30% lower than those for the hypothetical case of dispersed nesters, emphasising that the predictions of Horn's model can be upheld even when its underlying assumptions are violated. This conclusion though suggests that the model may be applicable under a broader range of circumstances than those originally proposed.

Aside from the theory, field data show that nesting colonies of the Great Blue Heron tend to be closer to points of minimum aggregate travel to all regional foraging areas than expected by chance (Gibbs 1991). Gibbs (1991) concluded that the spatial arrangement of wetlands limited the availability of sites with efficient access, favouring a clumped nesting pattern. A similar situation is found in the Osprey *Pandion haliaetus* when flight distances are averaged out over all colony members (Hagan III & Walters 1990). However, the use of marked males revealed that each individual would actually be better off by nesting near its preferred feeding sites and so the hypothesis was deemed to be an unlikely mechanism leading to aggregation (Hagan III & Walters 1990). The hypothesis is also disputed by observations of Bearded Tits, as the distances flown to foraging grounds by solitary and colonial nesters show no obvious difference (Hoi & Hoi-Leitner 1997).

Even though comparative studies often support the idea of a continuum from territorial to colonial nesters according to the degree of spatio-temporal variation in the food supply (Crook 1965; Erwin 1977), the use of marked individuals suggests Horn's hypothesis may not be able to account for the evolution of these systems through individual selection. Horn's hypothesis would need to invoke other constraints to explain the degree of aggregation seen in more continuous nesting habitats.

1.4.4 Information-centre hypothesis

A hypothesis which has been widely studied and much debated is the information-centre hypothesis (ICH) proposed by Ward & Zahavi (1973) to explain the evolution of bird assemblages in general. They suggested that colonies and roosts could function as meeting points where unsuccessful foragers could learn the location of food sources from successful foragers. Active communication may not be necessary as any cue that increases a bird's foraging success gained at a colony or roost, qualifies as information exchange because it reduces the recipient's uncertainty (Waltz 1982; Rabenold 1987). The reason why a successful forager should pay the cost of a return trip from the food patch to the colony or roost, and suffer the costs of being followed by unsuccessful parasitic foragers, is not clear (Rabenold 1986; Richner & Heeb 1995). An assumption of the ICH is that food patches are scarce and ephemeral but contain an abundant food source, so that attempts by the followed bird to dissuade or misdirect the follower are not selectively advantageous (Waltz 1982; Richner & Heeb 1995). Also, Brown (1986) considers that for an information-centre to evolve, the relative success of different individuals must change regularly, otherwise the ICH is a group selectionist hypothesis (Weatherhead 1983; Richner & Heeb 1995; Richner & Heeb 1996). In Cliff Swallows, no birds are mainly followers, leaders, or solitary foragers, suggesting that all colony members benefit about equally from the opportunities to receive information (Brown 1986). Zahavi (1996) considered that even a satiated bird would join a group in order to obtain information it might require in the future, so that information-centres could evolve from selfish interests. Thus, being part of an assemblage may function as an insurance against future food shortage (Zahavi 1996). For example, in a 3 year study of Rooks at a winter roost it was found that on most mornings, Rooks returned directly to their colony home range to feed (Feare *et al.* 1974). However, in periods of deep snow they fed with the members of other colonies at more localised food sources (grain stacks).

Some workers suggest that reciprocal altruism between closely related individuals is the only mechanism by which an information-centre could evolve. This would increase the inclusive fitness of the successful foragers, outweighing the costs of sharing (Hamilton 1964; Erwin 1978; Waltz 1982). It could also function between close cohorts of unrelated individuals, and observations of marked Black Vultures *Coragyps atratus* support these ideas, with mates, parents, offspring and certain families maintaining close contact at roosts throughout the year (Rabenold 1986). These associations are not simply a consequence of natal philopatry but reflect the daily reassembly of coalitions at communal roosting sites (Parker *et al.* 1995). However, close association of related individuals or the formation of coalitions is thought unlikely to occur in most breeding colonies and among the mobile membership of larger roosts (Richner & Heeb 1995).

The ICH was derived mostly from circumstantial, comparative evidence used to dismiss nest-site-limitation and predation hypotheses (Zahavi 1971; Ward & Zahavi 1973; deGroot 1980). For example, offshore feeding seabirds having larger colonies than inshore feeders (Lack 1968; Erwin 1977; Erwin 1978), is considered to be evidence of the value of information (Clode 1993). Using a similar logic, Ward & Zahavi (1973) suggested that bird roosts become larger due to an increased need for information as food resources become scarce. Roosting aggregations of the Rook become progressively larger after the breeding season, so that by winter, roosts may contain many thousands of individuals which converge upon a site from up to 45 km (Coombs 1961b; Patterson *et al.* 1971; McKilligan 1980). This seasonal increase in aggregation fits with the scenario envisaged by Ward & Zahavi (1973). However, the period of greatest food shortage for the Rook does not appear to be in winter. Instead, it is in June that competition for food probably causes the highest natural mortality of first year birds and greatest loss of adult condition (Holyoak 1971; Feare *et al.* 1974; Patterson *et al.* 1988). This suggests roosts should be largest in summer when information on food resources would be at a premium. This conclusion though needs to be balanced against possibilities such as the young being unable to fly the distances required to form large roosts, or foragers not being able to benefit from information about the food supply because it is uniformly scarce or because of the larger ratio of inexperienced (parasitic juveniles) to experienced (adult) foragers.

Other evidence offered in support of the ICH includes the relationship between breeding success and colony size or nest position within a colony. For example, Brown (1988), showed that breeding success in Cliff Swallows increased with colony size outside of the effects of local habitat quality, cautioned by Bayer (1982). This finding though may not have been due to information exchange, but rather to other uncontrolled factors which covary with colony size (Shields 1990). In contrast, the risk of fledgling starvation in Fieldfares actually increases with colony size (Wiklund & Andersson 1994). With respect to positional effects, Horn (1968) observed that nestling Brewer's Blackbirds *Euphagus cyanocephalus* at the centre of a colony gained more weight per day than young in peripheral nests. He suggested that this was because central birds have more neighbours from which they could learn the location of food patches. Alternatively, higher quality individuals may have bred at the centre of the colony as found in Kittiwakes *Rissa tridactyla* (Coulson 1968).

These examples demonstrate how comparative observational evidence may be insufficient to justify the ICH as many explanations are possible (Richner & Heeb 1995).

Experimental tests of the ICH also offer little conclusive support as nearly all published examples can be accounted for more parsimoniously through alternative explanations, such as solo foraging, local enhancement, network foraging (Hiraldo *et al.* 1993), or joint commuting (Bayer 1982; Mock *et al.* 1988). For example, the recruitment of birds to bait sites or food locations (Krebs 1974; Emlen & Demong 1975; Greene 1987; Brown 1986; Brown 1988; deGroot 1980; Loman & Tamm 1980) can equally be explained through simpler coarse-level local enhancement effects (Krebs 1974; Evans 1982; Flemming *et al.* 1992; Pöysä 1992; Richner & Heeb 1995; Buckley 1996; Buckley 1997a; Buckley 1997b) which have been shown to operate in all species, including Rooks (Waite 1981; Chantrey 1982), for which the ICH has been suggested to operate. The conflicts over interpretation of the evidence stem mainly from the difficulty in evaluating the distance over which organisms can perceive food, the sights and sounds of conspecifics, or those that are otherwise associated with the food source (e.g. a tractor ploughing a field) (Evans 1983; Mock *et al.* 1988).

The most conclusive evidence for the ICH comes from Black Vultures where naive birds follow knowledgeable ones to carcasses from communal roosts (Rabenold 1987; Buckley 1997a). This happens relatively rarely however compared to the other social foraging strategies, and using the same experimental protocols does not appear to function in the Turkey Vulture *Cathartes aura* which also roosts communally (Buckley 1997a).

Therefore, a simpler hypothesis to explain the evolution of communal nesting or roosting is that these aggregations concentrate foragers in space which leads to more rapid discovery of food patches via social foraging and local enhancement strategies than if foragers bred in a dispersed fashion (Buckley 1996; Buckley 1997a; Buckley 1997b). The suite of behaviours the ICH requires implies that information exchange is more likely to evolve after communal breeding or roosting is established (Mock *et al.* 1988) perhaps in more specialised situations as found for example, in the Black Vulture (see above: Rabenold 1986; Rabenold 1987; Parker *et al.* 1995).

1.4.5 Recruitment-centre hypotheses

Local enhancement is a form of cueing on conspecifics whose presence at the food source provides information on its location (Chantrey 1982). Through the use of models, Buckley (1996 & 1997b) hypothesised that aggregations concentrate foragers in space leading to a more efficient use of local enhancement than if birds remained separate and dispersed. This increase in foraging efficiency through passive recruitment from a point source is thought to explain the evolution of bird assemblages. However, the models showed that foraging efficiency is improved still further if individuals *actively* recruit others to form foraging groups (Evans 1982; Richner & Heeb 1995; Richner & Heeb 1996; Buckley 1996; Buckley 1997a; Buckley 1997b). These ideas differ in a subtle way from the ICH in terms of the mechanism proposed, as they offer an advantage to the individual in returning to an assemblage and having followers. The focus for the transmission of information is shifted from the assemblage to the food patch (Evans 1982; Richner & Heeb 1995). The individual gains from having more foragers with it, because this increases its mean rate of ingestion (Krebs 1974; Waite 1981; Chantrey 1982; Brown 1988) and decreases variance in foraging success, thus reducing the risk of starvation for the individual and its offspring (Krebs 1974; Ekman & Hake 1988; Flemming *et al.* 1992). This may be due to reduced risk of predation and reduced vigilance times at the patch (Elgar 1986), better search efficiency (Flemming *et al.* 1992), or other social foraging advantages such as prey confusion or prey tracking which are more dependent on the prey type involved (Mock *et al.* 1988; Brown *et al.* 1991).

As proposed for the ICH, these two hypotheses would only be expected to function where there is a high ephemerality of relatively rich food patches. Under such conditions searching individuals may be widely dispersed, making it likely that recruitment at the colony is more efficient than recruiting locally, or waiting at the food patch for other birds to join (Buckley 1996a; Buckley 1997b).

Of the two recruitment hypotheses, the idea of active recruitment gives a possible explanation for the displays seen at communal sites, such as the "weddings" above Rook colonies, or the great vortices of birds above roost sites. Zahavi (1996) however does not see why one individual rather than another should invest in a communal display to recruit a flock, suspecting the argument is group selectionist and that an individual would gain more by letting others recruit a flock and then joining it. This theoretical weakness is refuted by experimental evidence demonstrating active recruitment to foraging flocks. For example, Cliff Swallows recruit colony members to food patches with a specific call, especially in poor weather conditions when insects are harder to find (Brown *et al.* 1991). Ring-billed Gulls *Larus delawarensis* (Evans & Welham 1985), Black-billed Gulls *Larus bulleri* (Evans 1982) and Ravens *Corvus corax* (Heinrich 1989) also recruit other individuals to foraging groups through calling. Even free-living, solitary House Sparrows *Passer domesticus* that discover a divisible food resource make a "chirrup" call to recruit other foragers before foraging themselves (Elgar 1986). This recruitment is shown to be based on an individual decision because sparrows which locate a non-divisible food resource tend not to chirrup. Also the chirrup call rate per individual is inversely proportional to flock size, suggesting flock members will recruit others, and that these do not have to be kin or familiar coalitions. The possibility that pioneer sparrows establish flocks in order to facilitate food finding can be dismissed in this case because the food has already been found (Elgar 1986). In addition to sound, visual displays may be used to recruit individuals to foraging groups, as suggested in the Osprey (Greene 1987).

Although the idea of recruitment-centres is currently popular, there is contradictory evidence regarding its functioning even within the same species. For example, Flemming *et al.* (1991) considered that the greater opportunity for social foraging resulted in the increased number of fledged young in colony nests compared to the solitary nests of Ospreys. This hypothesis though, like the ICH and Horn's (1968) geometric model, is nullified by the findings of specific male feeding areas or territories (Hagan III & Walters 1990), as can occur also in the Great Blue Heron (Mock *et al.* 1988; Gibbs 1991). Under these systems of food exploitation, information exchange of any sort would appear to be useless. Prior & Weatherhead (1991) found that there may be only very limited benefits from information transfer in Turkey Vultures, as socially dominant individuals monopolise food patches which limits any benefits to those with the greatest need for food information. Also, in evidence against the recruitment-centre hypotheses, there does not appear to be social facilitation of food-finding in Swallows (Møller 1987) or Sand Martins *Riparia riparia* (Hoogland & Sherman 1976; although see Emlen & Demong 1975), even when food is in short supply.

In conclusion, it seems that information exchange via the ICH or recruitment-centre hypotheses grade into each other and may well be operating simultaneously (Rabenold 1987). The differences between these hypotheses are subtle and their predictions may overlap, which can cause problems for tests designed to discriminate between them (Mock *et al.* 1988). A combination of these hypotheses may also be used to explain bird assemblages (Barta & Szép 1995). For example, Richner and Heeb (1995) suggest that communal sites function as recruitment centres for successful foragers, and as information centres for unsuccessful ones, with the recruitment centre function being at the origin of the evolution of these assemblages. Richner and Heeb (1995) consider that the ICH mechanism is only one among several mechanisms that predict information transfer at a colony and that compared to the other mechanisms, it is the least likely to explain the evolution of coloniality.

Coupled with the siting of nests, it seems that there may be many means by which birds use their food resources more effectively by nesting colonially (Bayer 1982).

1.4.6 Two-principal-strategies hypothesis

Perhaps to overcome the shortcomings of the ICH mechanism in terms of individual selection, Weatherhead (1983) proposed the two-principal-strategies hypothesis. In its original form it was applied only to roosting assemblages. Weatherhead (1983) suggested that not all individuals participate in a roost for the same reason. More specifically, because dominance status is related to food-finding ability, subordinate birds use roosts to identify and follow dominant individuals to food. The dominant birds tolerate this information parasitism because their social status affords them access to central (or higher) perches which are buffered from predation by the surrounding subordinate individuals in the roost (Weatherhead 1983; Richner & Heeb 1996). Such a system could be employed by Rooks, as the older dominant individuals occupy higher positions in roost trees than younger subordinates which are more vulnerable to predation (Swingland 1977). The older birds supplant others at food sources, and so in spite of the parasitism of their knowledge or ability, they suffer little cost and are able to roost in these thermally sub-optimal positions (Swingland 1977). This relationship between roosting and feeding dominance is also found in mixed-species roosts of egrets and herons (Weatherhead 1983). Chough *Pyrrhocorax pyrrhocorax* (Still *et al.* 1986) and Starling *Sturnus vulgaris* (Summers *et al.* 1987; Feare *et al.* 1995) roosts both show the spatial segregation of age classes, and in Black Vultures juveniles tend to follow adults from roosts (Rabenold 1987). Thus this system may function in these species, although it is difficult to envisage the predators from which adult Black Vultures gain protection by roosting with juveniles (Ward & Zahavi 1973).

This hypothesis could perhaps be extended to breeding colonies to explain their formation. For example, older Purple Martins *Progne subis* nest in the higher tiers of "Martin houses", thus reducing the likelihood of predation from climbing predators when the lower tiers are occupied by younger birds (Morton & Derrickson 1990). Although untested, the 1st and 2nd year birds may perhaps gain from following older individuals to food.

With strict application of this hypothesis, however, it is difficult to see how it could operate where: central nests are less successful than peripheral nests (Least Tern *Sterna albifrons*: Brunton 1997); the decreased breeding success of lower quality peripheral birds is not due to predation (Kittiwake: Coulson 1968); younger birds are not found at the edge of the colony (Osprey: Hagan III &

Walters 1990); or no difference in foraging strategy across the colony is recorded (Cliff Swallow: Brown 1986).

The two-principal-strategies hypothesis could link predation benefits to any of the information exchange hypotheses, and so any of the evidence against information or recruitment-centre functioning outlined above, is also evidence against this hypothesis.

Thus it seems unlikely that the two-principal-strategies hypothesis could explain the evolution of coloniality, although the idea of two or more interacting strategies may be applicable.

1.4.7 Hidden-lek/EPC hypothesis

Wagner (1993) suggested that aggregations of breeding individuals, including the clustering of all-purpose territories (Kendeigh 1941; Darling 1952; Orians 1961; Stamps 1988), may form in response to females seeking extra-pair copulations (EPCs). As such, this hypothesis does not relate to the formation of communal roosts. The hypothesis suggests colony formation is female-driven, with males being drawn to colonies by females seeking EPCs. The term "hidden-lek" is derived from the skew in extra-pair fertilisation (EPF) success among older males, which matches the skew in male mating success typical of leks (Wagner *et al.* 1996). It was originally proposed that males gained these advantages at colonies through forced copulations (Morton & Derrickson 1990). However, female solicitation has become the emphasis of this hypothesis (Wagner *et al.* 1996; Hoi & Hoi-Leitner 1997). This is supported by detailed studies of the Bearded Tit where, regardless of mate quality, high-quality females settle in colonies and low-quality females settle solitarily (Hoi & Hoi-Leitner 1997). High-quality females are thus thought to incite male-male competition for

EPCs so that they secure EPFs from high-quality males. The actual costs and benefits of EPCs differ for males and females and are difficult to assess (Wagner 1992), especially when these complex mating strategies are age dependent (Møller 1987; Wagner *et al.* 1996). For example, Røskaft (1983) found that young female Rooks copulated significantly more with promiscuous males than old females suggesting that male Rooks achieve a selective advantage by pursuing a mixed mating strategy, so that besides being strongly monogamous, they are also promiscuous.

Males are able to reduce the apparent cuckoldry cost of social living through mate guarding or by increasing the frequency of within-pair copulations (Møller & Birkhead 1993). However, the positive relationship between the uncertainty of paternity and the degree of sociality as measured by the frequency of EPCs in comparative analyses suggests the males of colonial species suffer from increased competition (Møller & Birkhead 1993). Rates of EPCs and EPFs are not necessarily synonymous however, and although within species EPFs increase with density, between species EPF frequencies are not correlated with nesting dispersion or local breeding density (Westneat & Sherman 1997).

Other strategies which may be associated with EPCs are intraspecific nest parasitism, and infanticide. Møller (1987) recorded infanticide as an important mortality factor, which increased with colony size in Swallows. Nest guarding during egg laying also increased with colony size perhaps due to the increased chance of intraspecific nest parasitism (Møller 1987). Intraspecific nest parasitism means females can also be cuckolded, and is recorded for colonial Bearded Tits (Hoi & Hoi-Leitner 1997), Cliff Swallows (Brown & Brown 1991), Eared Grebes *Podiceps nigricollis* (Lyon & Everding 1996) and Starlings (Pinxten *et al.* 1993). Intraspecific nest parasitism and infanticide have not, however, been recorded in Sand Martins (Hoogland & Sherman 1976).

1.4.8 Social stimulation/facilitation hypothesis

Although one of the original hypotheses of colony formation, this hypothesis is dealt with last because it can incorporate the benefits associated with most of the others.

Darling (1938) thought that the members of a species clump together in order to increase social stimulation and synchronise breeding behaviour. Synchronised production of young can swamp potential predators thus reducing the probability that offspring will be preyed upon (Orians 1961; Patterson 1965; Feare 1976). Synchrony may also allow for the exploitation of a short duration food supply (Orians 1961), increase feeding efficiency through social foraging and information transfer effects (Emlen & Demong 1975), and affect the ability of birds to capitalise on extra-pair matings (Emlen & Oring 1977; Stutchbury & Morton 1995; Weatherhead 1997).

However, breeding synchrony is not always correlated with colony size (Snapp 1976; Orians 1961; Hoi & Hoi-Leitner 1997), or reproductive success in terms of losses due to predation or food shortage (Snapp 1976; Hagan III & Walters 1990).

Overall, it is believed that where social stimulation effects operate, they are probably a result, and not an evolutionary cause, of coloniality (Orians 1961; Hoogland & Sherman 1976).

1.5 Colony size variation and a new hypothesis of colony formation

The factors identified as important to the evolution of coloniality often appear to favour colonies of certain sizes, and yet size variation still persists (Brown *et al.* 1990). The cost/benefit appraisal of the selective forces acting on colonies of varying sizes has led to little progress in the understanding of size variation (Brown *et al.* 1990) and the evolution of coloniality in general (Danchin & Wagner 1997). The costs and benefits identified often differ between species and even between populations of the same species (Hoogland & Sherman 1976; Snapp 1976; Møller 1987; Wiklund & Andersson 1994). Separate hypotheses to those proposed to explain the evolution of coloniality have therefore been advocated to explain variation in colony size. The simplest of these considers that individuals distribute themselves amongst colony sites according to an ideal free (IDF) distribution, whereby the fitness returns for all individuals are equal (Brown *et al.* 1990). Thus, assuming equal competitive ability amongst individuals (Milinski & Parker 1991), colony size will vary in proportion to food availability due to competition and habitat patchiness. The negative relationship of neighbouring colony sizes upon one another has been recorded (Furness & Birkhead 1984; Hunt *et al.* 1986; Ainley *et al.* 1995), as has the more direct positive effect of foraging habitat on colony size (Møller 1987; Gibbs *et al.* 1987; Bustamante 1997). However, because the costs and benefits of being a colony member often vary with colony size, there is likely to be a departure from the IDF distribution (Sibly 1983; Brown *et al.* 1990). The colony size optima may vary for each individual according to its abilities such that certain classes of individuals settle in certain sites or colony sizes (Jones 1987; Hoi & Hoi-Leitner 1997), perhaps due to despotic effects (Robinson 1986). An IDF distribution of foragers amongst patches will also be affected by the amount of information an individual can gather about the foraging habitat and potential competitors, and the rate it can be obtained in relation to the rate of change in the environment (Brown *et al.* 1990; Milinski & Parker 1991). Finally, social attraction effects may operate so that larger colonies become larger than expected (Danchin & Wagner 1997).

As Brown *et al.* (1990) noted, "any general theory for the evolution of coloniality should account for colony size variation and for the choices individuals make that lead to this variation." Danchin & Wagner (1997) have taken a bottom-up approach to this problem by investigating the factors involved in individual choice. They suggest that coloniality has evolved due to social attraction through conspecific cueing, with individuals selecting habitat based on the presence of conspecifics. This has already been recognised as a mechanism for aggregation in many species (Siegal-Causey & Kharitonov 1990; Stamps 1988; Podolsky & Kress 1989; Brown & Rannala 1995). Individuals nest as closely as possible to conspecifics with high fitness in order to benefit from the same favourable conditions (Danchin & Wagner 1997). Fitness may be assessed via reproductive success (Boulinier *et al.* 1996), which offers a combined measure of the costs and benefits associated with a particular site. This may explain why young Rooks which continue to visit a rookery until the end of the breeding season in May are more likely to return there to breed in their second year than those seen only in March and April (Patterson & Grace 1984). In Lesser Snow Geese *Chen caerulescens*, it has been shown that shifts in colony location can occur as a result of new recruits settling where reproductive success is highest (Ganter & Cooke 1998).

The problem with this hypothesis is that it offers no mechanism for the establishment of new colonies through direct estimation of habitat potential. In the American White Ibis *Eudocimus albus*, for example, colonies can sometimes be established at novel locations in response to the prevailing feeding conditions (Kushlan 1976). Even though adults may move in response to poor reproductive success (Beletsky & Orians 1991), this finding requires direct assessment of the habitat which could not be based on previous reproductive success. Therefore, it is possible that two strategies of habitat choice operate, with individuals originally settling at a site in relation to the local resources and then in relation to the number of individuals present (Brown & Rannala 1995). Recruits may continue to settle at a colony to the detriment of those already present, if the advantages of joining the group are deemed to be higher than for joining other groups or nesting alone (Sibly 1983).

The degree to which social attraction, or other site choice effects operate is best assessed against the background of the relationship of colony size to local variation in foraging resources. The variance left unexplained in such IDF models could then give an indication of the extent to which other hypotheses operate and the IDF distribution is violated.

1.6 GIS terminology and procedures used throughout this thesis

The GIS used was either Arc/Info (version 7.0.3, ESRI 1995) or ArcView (version 3.0, ESRI 1996). Within a GIS, data are stored as “coverages”, which are separate digital representations of the themed data layers depicted on many maps. These coverages can be transformed between “vector” or “grid” format depending on the required speed and resolution of the querying process. The features present in coverages depict spatial positions which can be given many descriptive (often time-linked) “attributes”. Sets of features can be selected based on either spatial position or descriptive attributes, depending on the question being asked. The spatial relationships of features within or between data layers can be downloaded for further analysis, which in this thesis was performed in SPSS (version 7.5.1, SPSS Inc. 1996), unless otherwise stated.

Chapter 2

2 Preliminary analysis of Rook distribution and abundance[1]

2.1 Aims

- Establish the effect of survey date on Rook colony nest counts as colonies will be counted across a large study area.
- Map and describe the spatial distribution of Rook colony sizes within the GIS.
- Define a "colony unit" by testing for spatial aggregation of the colonies mapped, and the possible interchange of individuals between colony sites between years.

2.2 Introduction

2.2.1 Effect of survey date on Rook colony counts

Surveys are an important means of identifying the population trends of a species through space and time. For robust comparison of numbers between sites and between years it is important to standardise survey effort as much as possible. National surveys of the Rook have been carried out in Britain from late March to late April (Sage & Vernon 1978; Brenchley 1986). Colony sites are usually traditional, being visited by Rooks throughout the year, making them easy to locate and count (Patterson, Dunnet & Fordham 1971). The majority of nests are blown out by winter, while those surviving are robbed for building material, leaving a good correlation between the number of nests occupied and the number extant during the breeding season

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[1] A version of the work presented here has been accepted for publication in *Bird Study*, as the paper entitled "Colonisation patterns at Rook *Corvus frugilegus* colonies: implications for survey strategies", by L.R. Griffin (proof copy provided in Appendix).

(Nicholson & Nicholson 1930; Brenchley 1986; Rutnagur 1990). Colony nest counts can change rapidly from one week to the next during the spring breeding period (Marshall & Coombs 1957; Rutnagur 1990). Previous studies have not considered how these changes in nest numbers may affect the comparison of nest counts from different dates. Therefore, a sample of colonies was monitored to test whether there was a period during which they were at their maximum and if they showed predictable increases through time. This would clarify the effects of a spread of survey dates upon nest counts arising from the need for a single observer to find and count all colonies over a large area. The data are also used to assess the effect of initial colony size on the synchrony of nest building and the number of nests added at a colony.

2.2.2 Yearly changes in colony size across the spatial distribution

Having quantified the effect of survey date on nest counts, the spatial distribution of colony size across the study area and the changes in nest numbers within colonies between years were analysed. This preliminary analysis of spatial structure was undertaken to elucidate whether or not small colonies tend to be near large ones, suggesting a competitive effect, or whether large colonies aggregate together, suggesting an attraction effect. Previous studies suggest a fairly even distribution of colony units, with clusters in some areas surrounded by areas relatively empty of other rookeries (Nicholson & Nicholson 1930; Patterson *et al.* 1971). The size of a rookery does not seem to affect the size of, or distance to, neighbouring colonies (Nicholson & Nicholson 1930; Marples 1932).

The relationship between year-to-year fluctuations in colony size and distance to neighbouring colonies was used to assess the likelihood of any interchange of individuals or groups between sites. On the basis of these findings, it was hoped that a colony unit could be defined in a more biologically meaningful way than the arbitrary rules used in previous studies, a problem that is fully acknowledged (Alexander 1933; Roebuck 1933; Lloyd 1939; Patterson *et al.* 1971).

2.3 Study area

Fieldwork was carried out over a contiguous area covering County Durham, and extending partly into the counties of Tyne and Wear and Cleveland, UK. The area of approximately 3000 km^2 is bounded by the River Tyne to the north and the River Tees to the south (Fig. 2.1). The study area rises from the coast in the east to the moorland hills and valleys of the Pennines in the west at 600 m. The eastern part has the largest urban areas and farming is predominantly arable. Westwards, the amounts of pasture and meadow increase.

2.4 Methods

2.4.1 Sample colony counts

Colonies were defined as any group of nests more than 100 m from any other such group (Patterson *et al.* 1971; Brenchley 1986). This definition allows for shifts in nest position between adjacent nest groups within this area, which appear to take place when nests are destroyed. The survey transect sampled 18 roadside colonies, located in deciduous woodland, up to

15 km from Durham City, UK. Nest counts were made every four days between 1 April and 25 April 1996. The colonies had a range of sizes representative of the area, based on nest counts made in spring 1995 (1996 range 5-136 nests, median = 25, *n* = 18).

For the initial visit to a colony, the position of each nest was mapped by standing directly beneath it and measuring the distance to its nearest neighbour, with angular positions with respect to one another being judged by eye. Trees were assigned a number and species code, and diagrams included other salient features such as walls, fences, ditches or streams. For distances greater than 5 m a tape was laid out under the colony, otherwise a meter rule was used to judge the distance. Note was also made of the nests built above one another. Where nests were tightly clumped the decision as to how many nests were present was based on the intersection of the circular outlines. On subsequent visits only nest losses or additions needed to be mapped onto these original plans of the colonies.

Nests were recorded as 'incomplete' (N_i) when light could be seen through the structure from underneath, or 'complete' (N_c) when this was not the case as the nest had been lined (Ena 1984).

Where it was possible to observe the nest building activities of the Rooks during the surveys (at one colony the birds were too wary) it was noted that some N_i were inactive relict structures from the previous breeding season. In contrast, the N_c were all active from the first survey date with single Rooks or pairs recorded at the nest. Thus, the N_c criterion was used in the calculation of nest numbers as this was likely to be the best index of actual increases in the number of breeding pairs at the colonies through time.

2.4.2 Colony size distribution

The whole study area was surveyed in 1995 and 1996, and a partial survey of a contiguous area was made in 1997. Colony counts in 1995 were made after 4 April based on a subjective assessment that nest numbers had reached an asymptote. In 1996 and 1997 all counts were made after 10 April based on the findings of the sample colony count procedure outlined above. Consistent decisions on compound nests and nest activity were aided by having only one observer throughout. Inaccurate counts due to access difficulties, large rookery size and counts made from a long distance were not applicable as all nest counts were made from beneath the nest trees. Also, for this reason, the small percentage of nests in conifers such as Scot's Pine (*Pinus sylvestris*) were not thought to pose a problem in this study (Brenchley 1986).

Colonies were located by following flight lines from winter roosts and from data collected in historical surveys (D. Sowerbutts pers. comm.). Also most of the study area is within 2 km of a road, and so colonies could be located using binoculars within this distance. With reference to landscape features, the areas searched were delimited by shapes drawn onto Ordnance Survey (OS) 1 : 25000 scale maps. This ensured complete coverage of the woodlands in the study area.

The co-ordinates of single nests or nest groups more than 50 m from any other such group were extracted from the OS 1 : 25000 scale maps and input as points into Arc/Info. This colony definition was chosen rather than that of 100 m used for the sample colony counts, because nest group differentiation needs to be as fine-grained as possible, considering the scale of the OS maps used, if the hypothesised movement of nest groups between years is to be detected. Also, the 50 m distance allows for the aggregation of points, whereas larger distance definitions could not be meaningfully divided if this was required.

2.4.3 Changes in colony size

Within the GIS, the nest counts for all three years were added as descriptive attributes to the points in the coverage generated, showing the spatial positions of the colonies.

2.5 Analyses

2.5.1 Sample colony counts

The change in nest numbers over the survey period (Fig. 2.2), was standardised by subtracting the initial N_c (and N_i) from the N_c (and N_i) for each colony for each date, and then dividing by the initial N_c (and N_i) recorded for that colony on 1 April. The standardised N_c percentages were then arcsine transformed before using a one-way ANOVA with Tukey's Honestly Significant Differences test to identify significantly different means (Sokal & Rohlf 1997).

To determine whether colonies increased by the same proportion, the initial N_c for each colony was subtracted from the N_c recorded for that colony on the modal date of maximum counts of all colonies. Thus, the time period over which the increases were compared was the same for each colony (Fig. 2.4).

Colonies were classified as 'small' (range 5-25 nests, median = 18, $n = 9$) or 'large' (range 26-136, median = 61, $n = 9$) if their maximum nest count during the survey period was less than or equal to (small colonies), or more than (large colonies) the overall median of 25. Differences in the percentage increases and the dates of maximum counts between these two groups were investigated using the Independent Samples *t*-test and the Kolmogorov-Smirnov two sample test (K-S Test), respectively. The Independent Samples *t*-test incorporates Levene's Test for the equality of variances which is used to determine the type of *t*-test performed.

2.5.2 Colony size distribution

The map of colony locations for 1996 was analysed for spacing patterns using a method based on Arc/Info commands. The points entered in the GIS represent the minimum possible definition of what constitutes a Rook colony considering the scale of the OS maps used. This definition can be altered by aggregating the points within a certain distance of each other to a new central location to represent the rookery. The colony points which are the building blocks for the next larger colony size definition are known as "colony units".

The method of aggregation assumes that colonies extend over circular areas with a 50 m radius. This distance is increased by 50 m for each colony point with each iteration of the program. Colony areas which intersect are assumed to represent a single colony unit and the locations of the original colonies within this area are combined to give a single central point. At the next iteration of the program this new location is given a colony area extending by a further 50 m and the process of colony aggregation is repeated. This method aimed to identify any distinct spacing categories in the distribution of the colonies, which would appear as "steps" in the resulting graph. The largest distance to which colonies were aggregated was 3 km, half the maximum nearest neighbour distance (6 km) between the original 50 m radius colony units.

Colony locations and sizes for all years were downloaded from the GIS and analysed in the GS+ package (version 3.06.5 Beta, Gamma Design Software 1998) using the Moran's I spatial autocorrelation index. Correlograms were produced as they take account of the variation in local means and variances of colony nest numbers, likely in such biological data, which can give misleading patterns in semivariograms (Rossi *et al.* 1992). Isotropic - rather than anisotropic - correlograms were produced as there was no *a priori* expectation of angular trends within the data. Moran's I is a product moment correlation of the attributes for all pairs of points in a distance class whose interpretation is similar to that of Pearson's correlation coefficient (Legendre & Fortin 1989). The Moran index is positive (maximum value of +1) when nearby areas tend to be similar in attributes, negative (maximum value of –1) when dissimilar, and approximately zero when attribute values are arranged randomly and independently in space (Goodchild, 1986). Plots of Moran's I values against distance gives the correlogram. A correlogram that has positive values of Moran's I at short lags and negative values at long lags indicates a distributional gradient. Oscillation between positive and negative values indicates a patchy distribution (Legendre & Fortin 1989).

2.5.3 Changes in colony size

Changes in colony size between the three survey years were calculated for consistent colony locations. Also, based on the results of this chapter, the effect of early counts on colony size was minimised, by comparing colonies counted after 9 April. Comparison of the same colony locations between years and the use of the cut-off survey date reduced the sample size below that attained for any one year. The correlation between yearly counts was measured using the Spearman rank coefficient (r_s). Changes in colony size from 1995 to 1996 were compared to those occurring from 1996 to 1997 using a t-test. Spearman rank correlations were calculated to assess whether changes in nest numbers were proportional to colony size. Also, the fluctuations in nest numbers between years within colonies was measured using Pearson correlations (r). The spatial distributions of these changes in colony size were compared for consistent colony locations for 1995 to 1996, 1996 to 1997 and 1995 to 1997 using Moran's index across a range of distance lags, with the production of isotropic correlograms.

2.6 Results

The area containing the subset of colonies counted around Durham City is shown in Figure 2.1. The other colonies and relative size classes are those mapped in 1996 when the sample colony counts had reached an asymptote.

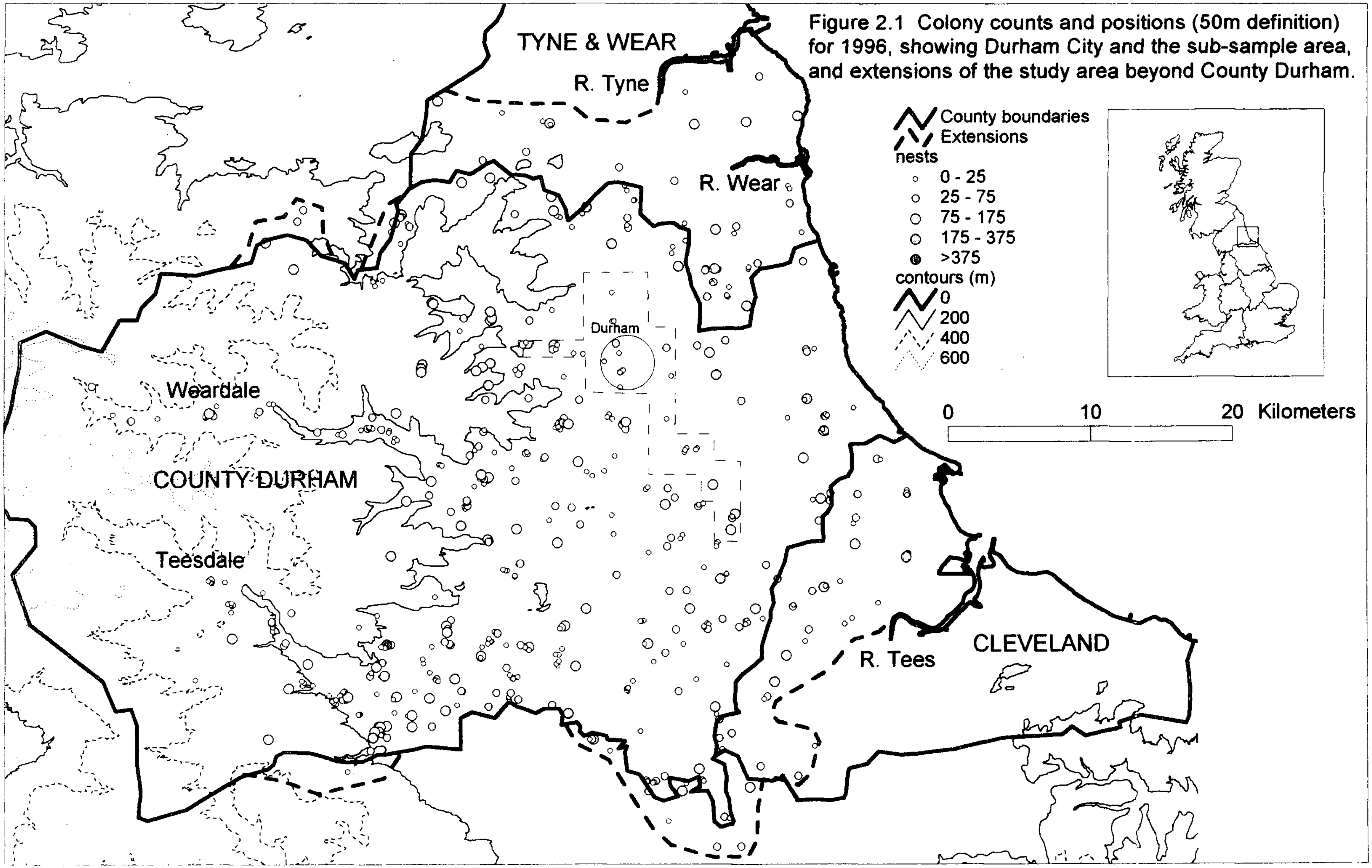


Figure 2.1 Colony counts and positions (50m definition) for 1996, showing Durham City and the sub-sample area, and extensions of the study area beyond County Durham.

2.6.1 Sample colony counts

The temporal pattern of change in the numbers of completed and incomplete nests was the same across all 18 colonies (Fig. 2.2). There was a significant difference in N_c between survey dates (ANOVA $F_{5,102} = 2.30$, $P = 0.003$). The Tukey test showed counts on 5 April were significantly lower than on the last three survey dates at $P = 0.05$, with no significant increases after 9 April, 1996. N_i showed an opposite but less marked trend over the same period, although the difference between the two measures is mainly due to some nests being started and completed between surveys with no N_i stage being recorded. Also, the colony nest maps showed that some N_i from the winter period remained until much later in the survey when they were completed or disappeared. Similarly, some N_c fell to the ground or returned to an incomplete state before disappearing.

Colonies were asynchronous in reaching maximum nest counts, with no single date encompassing all colonies at their maximum. Most colonies, 14 (78%), were at their maximum on 21 April, and 7 (39%), first peaked at this time (Fig. 2.3). There was no significant difference between 'small' and 'large' colonies with respect to the dates on which they first reached their maximum number of nests (K-S Test $D_{9,9} = 0.471$, $P = 0.979$). Colonies increased significantly from their initial counts up to the modal date of maximum counts on 21 April across the range of colony sizes ($r_s = 0.79$, $P < 0.01$; Fig. 2.4). The percentage increases at 'small' colonies did not differ significantly from those at 'large' colonies (t-test assuming unequal variances $t = -0.876$, df = 8.532, $P = 0.405$), although 'small' colonies were more variable (range 0-80%) than 'large' colonies (range 13-30%) (Levene's

Test $F_{1,16} = 15.04$, $P = 0.001$). The overall mean percentage increase up to 21 April was 24%.

2.6.2 Colony size distribution

The rookery distribution extends from the coastal areas through the lowlands up to 400 m in the west along the agricultural corridors of the Wear and Tees valleys. The surrounding moorland areas are uncolonised as are other patches within the lower lying areas (Fig. 2.1). The largest colonies show a tendency to be towards the edges of the distribution and there is a suggestion of some clustering of the colony units (Fig. 2.1). The clustering of colonies is shown by the large reduction in colony units achieved by aggregating colonies up to 200 m apart (Fig. 2.5). There is little suggestion of any further patterns of spatial aggregation, although there is a slight change in the slope of the curve at about 1 km, with further small changes thereafter.

The correlogram of Moran's I coefficients shows some deviation from the zero correlations expected for a random distribution of colony sizes for 1996 (Fig. 2.6). This is also the case for the colony data for 1995 and 1997 (not presented).

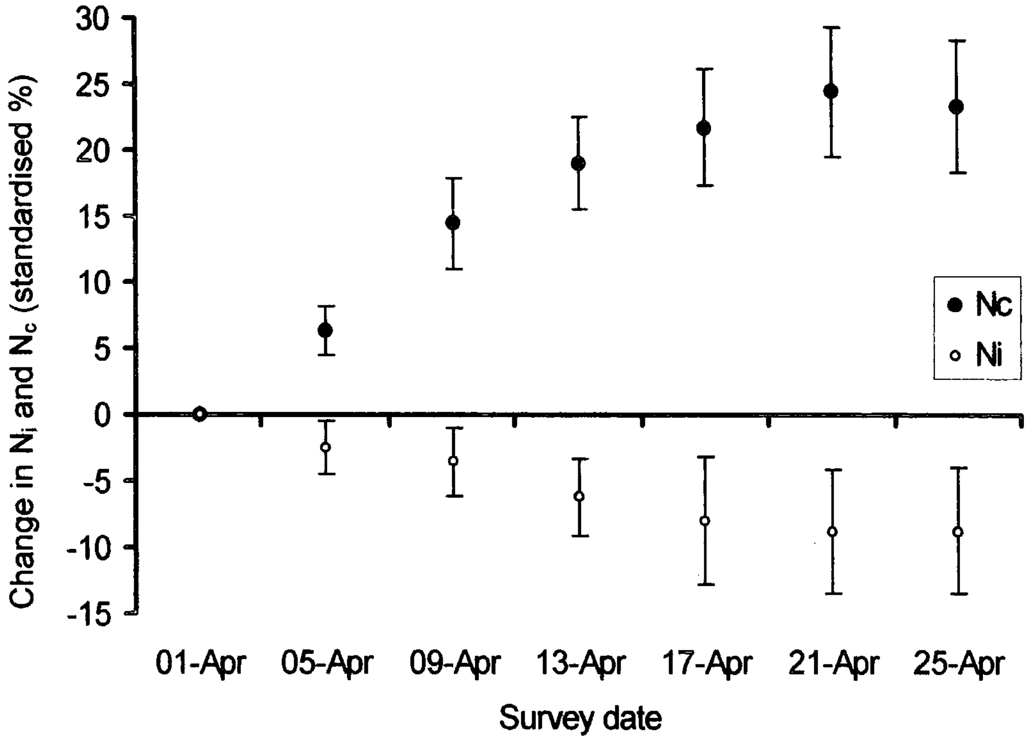


Figure 2.2 Change in number of incomplete (N_i) and complete nests (N_c) as standardised mean (± se) percentages of initial counts for the survey period in April, 1996. The initial totals of N_i and N_c for the 18 colonies on 1 April are 36 and 643, respectively.

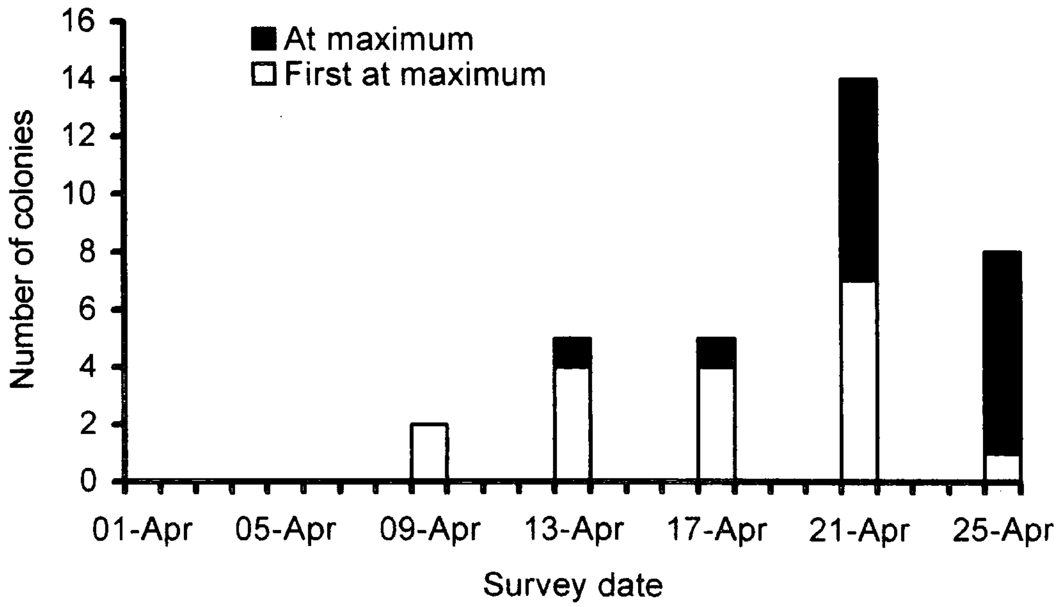


Figure 2.3 The survey date in 1996, on which colonies first reached their maximum number of complete nests (N_c) and the number of colonies sustaining this count.

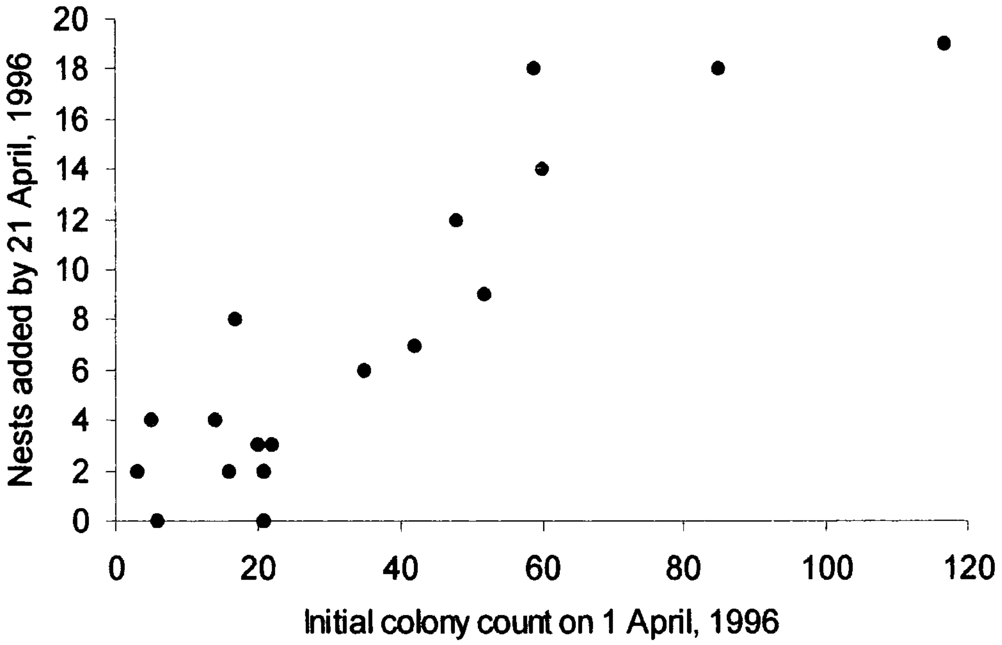


Figure 2.4 The increase in the number of complete nests (N_c) at each of the 18 colonies from 1 April 1996 to the modal date of maximum nest numbers on 21 April 1996.

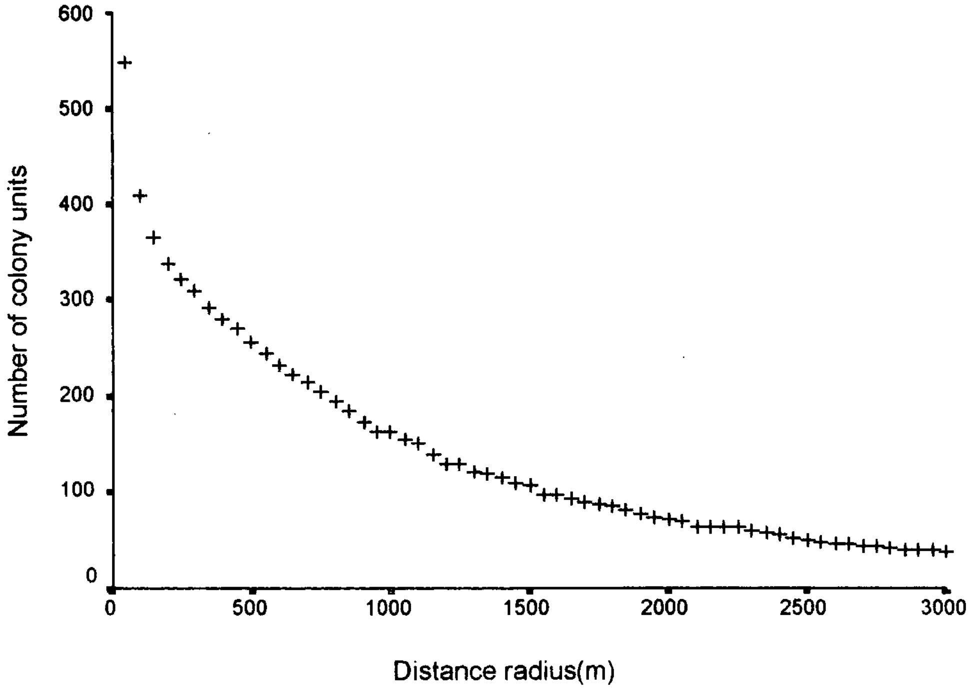


Figure 2.5 Change in the number of 'colony units' at 50 m aggregation increments of colony definition. Colony units closer than twice the distance radius are aggregated into a single colony unit before the process is repeated.

2.6.3 Changes in colony size

The general hierarchy of colony sizes in the study area was maintained between consecutive years (1995-96 $r_s = 0.95$, $P < 0.001$; 1996-97 $r_s = 0.91$, $P < 0.001$) with little drift over the three seasons. From 1995 to 1996, the selected set of 279 colonies generally increased in size (mean change in absolute number of nests $\bar{x} = 3.4$), whilst from 1996 to 1997 counts across the same 279 colony locations decreased ($\bar{x} = -3.0$). The changes in nest numbers differed significantly between years ($t = 6.46$, df = 556, $P < 0.001$), with the overall change from 1995 to 1997 being slightly positive (Fig. 2.7).

There was a significant positive correlation between colony size and the change in nest numbers at a colony from 1995 to 1996 ($r_s = 0.16$, $P < 0.01$). Colonies generally increased by 10% from 8998 to 9935 nests in total. The reverse was true in 1997 with a -8.3% decrease to 9109 nests ($r_s = -0.41$, $P < 0.001$). Colonies that increased from 1995 to 1996 were mainly those that decreased in 1997 ($r = -0.16$, $P < 0.01$).

The Moran index of autocorrelation in nest changes between years at colony locations showed no consistent pattern across the lag distances (not presented). The spatial pattern of changes from 1995 to 1996, for example, shows no geographic trends independent of the tendency for larger colonies in the west to increase by larger amounts (Fig. 2.8).

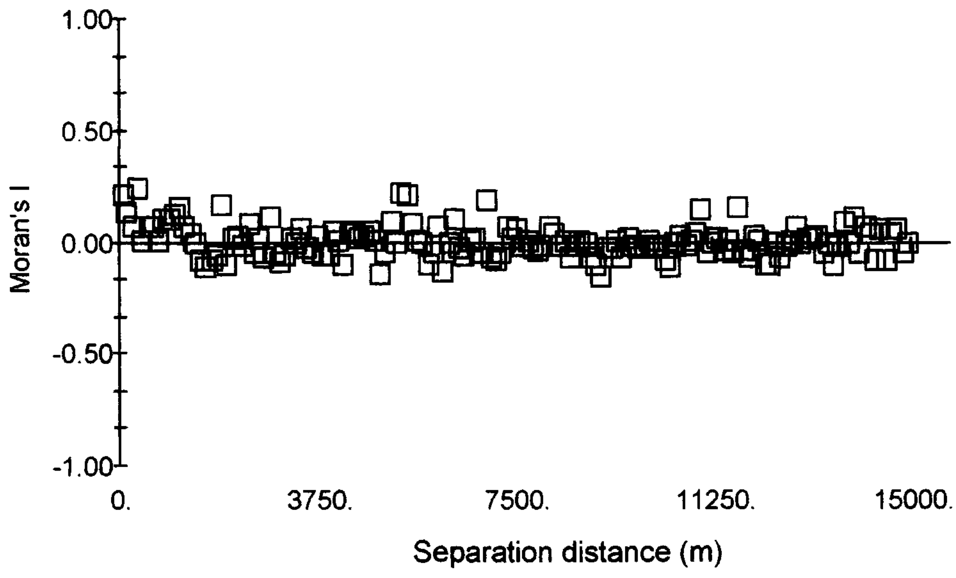


Figure 2.6 Isotropic correlogram of Moran's I with distance for the 1996 distribution of colony counts.

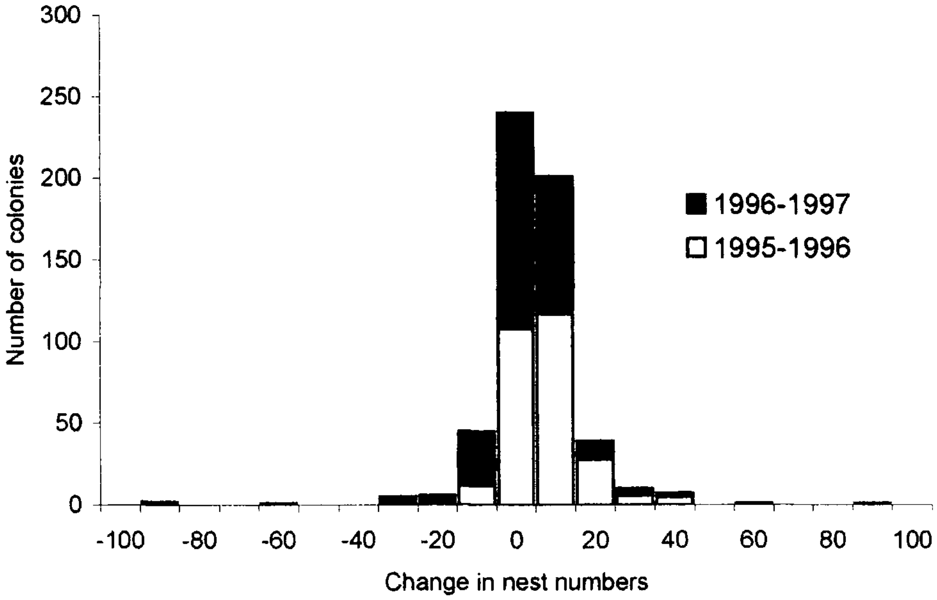


Figure 2.7 The change in nest numbers between years at consistent colony locations from 1995 to 1997.

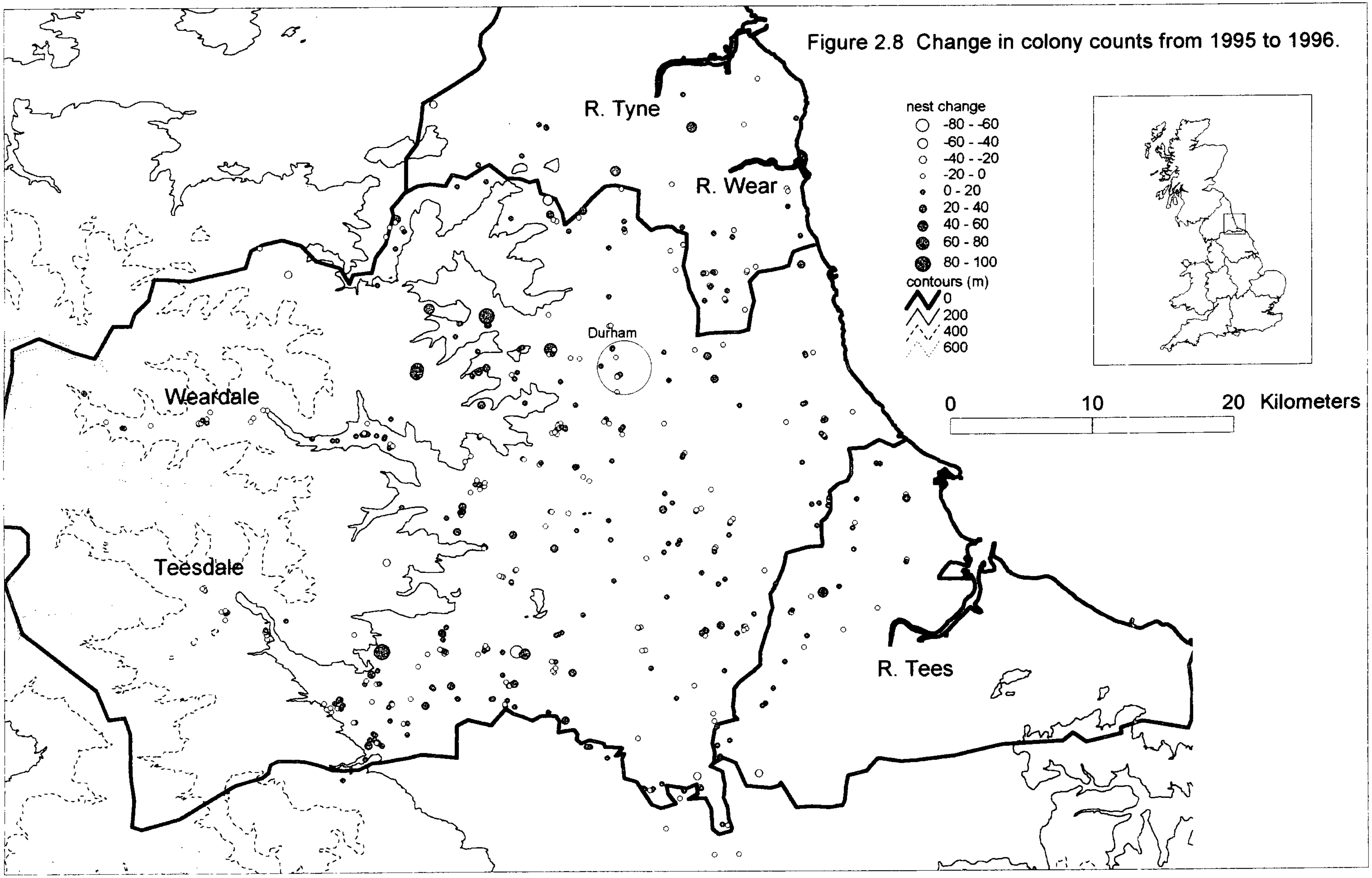


Figure 2.8 Change in colony counts from 1995 to 1996.

2.7 Discussion

2.7.1 Sample colony counts

The dynamics of nest numbers in a sample of colonies was measured as a basis for assessing the comparability of nest counts from a span of survey dates. The dates covered the weeks previously recommended for survey (Mitchell 1976; Sage & Vernon 1978). Increase in nest numbers during March was not determined, although extrapolation from Figure 2.2 suggests little difference to the spring build-up noted in other regions (Alexander 1933; Cramp & Ward 1936; Marshall & Coombs 1957).

The significant increases in colony size until the second week of April suggest that comparison of counts should consider only those made within the asymptote period after 9 April. If not, as in Brenchley's (1986) study where counts from late March and early April were used to make inferences on how the rook population had changed, a correction factor should be applied. The present study shows that colonies may be at 80% or less of their potential maximum size at the beginning of April. Thus the errors in comparisons of colony counts with historical survey data or within a large study area surveyed over a number of weeks may be considerable. Establishing the presence of an asymptote period in nest counts and the application of correction factors would go some way to overcoming this problem although this assumes a common pattern of nest increase between years. Previous work suggests this may not be the case as climatic conditions preceding the breeding season can affect the build-up of nest numbers and would need to be taken into account (Marshall & Coombs 1957).

Smaller colonies showed greater variation in the date at which they reached their maximum counts and in the percentage increases that occurred. Both parameters suggest that smaller colonies (<25 nests) may be less synchronous than larger ones (>25 nests) across the colony sub-sample area (as shown in the Gull-Billed Tern *Gelochelidon nilotica*, Møller 1981), although this may be due to the effect of colony size on the sensitivity of the measures used, especially in the case of percentage increase. The constant pattern of nest increase seen across the colonies suggests the processes of colony build-up are similar at 'small' and 'large' colonies within the range of colony sizes sampled in this study.

2.7.2 Colony size distribution

When the counts of the sample colonies reached an asymptote in 1996 the additional colonies in the area were counted. Thus differences in colony size are thought to reflect real differences rather than an artefact of the sampling procedure. The larger colonies at the edge of the geographical distribution suggest that conspecific competition may be an important factor determining rookery size, as these colonies are not surrounded by potential competitors. A similar situation has been recorded in The Isle of Man (Williamson & Cowin 1940) and the Wirral Peninsula (Marples 1932). This hypothesis of competition should be more obvious at local levels (Ainley *et al.* 1995). However, the correlogram for 1996 (Fig. 2.6) (as for 1995 and 1997) shows that small colonies do not necessarily occur next to large ones and that large or small colonies can occur together. This lack of 'negative size structuring' (Furness & Birkhead 1984) suggests that competition alone is not ordering the distribution of colony sizes. The reasons for the correlogram showing no strong positive or negative structure at any scale is probably because it does not take into account the direct effects of habitat heterogeneity on colony sizes. The landscape is obviously structured on different scales (Wiens 1989). From east to west the study area changes from predominantly tilled land through a greater percentage of pastures and meadows in the west up to moorland at higher altitudes. This is a geographic trend which may affect colony sizes. For instance, rookeries do not occur on the moorland area probably because of a lack of suitable foraging and nesting habitat. More locally, within an agricultural region there is clumping of similar field types which may make some areas more suitable than others. The oscillations between positive and negative values in the correlogram for 1996 suggests a patchy distribution of the Rooks which may be a response to the patchy nature of the landscape (Legendre & Fortin 1989).

The colonies have a clumped distribution at a 50 m colony definition (Fig. 2.5). When aggregated to colony units of 200 m or greater (i.e. more than 400 m from neighbours), this clumping is greatly reduced and colony units are randomly dispersed. Based on this aggregation, it was decided that in order to reduce computation times in more complex analyses carried out later in this thesis, colonies up to 500 m apart could be considered as single 'units'. From field observation it is clear that the definition of a rookery on the basis of a 100 m separation is useful for survey strategies but has little relevance to what the Rook perceives as a breeding colony. Rookeries up to about 1 km apart often intermix when feeding, displaying above nests or going to roosts (pers. obs.; Coombs 1961; Patterson *et al.* 1971; Barnes 1997). These clumps of colonies often occur around the peripheries of towns as though an original central location has been scattered, perhaps through disturbance, as the town expanded.

2.7.3 Changes in colony size

The effects of 'early' or 'late' springs (Marshall & Coombs 1957) on between-year comparisons of nest numbers could have been minimised by following the sample colony count procedure outlined above. This, though, was prevented in 1995 and 1997 by time constraints. Instead, a subjective assessment of colony build-up was made (Harris & Forbes 1987). It was thought that 1995 may have been an earlier season, with 1997 being similar to 1996. Thus only colonies counted after 9 April were compared as it was felt that this encompassed the asymptote period in all years.

The general hierarchy of colony sizes was consistent between years of population increase or decrease. Across a span of survey years gradual shifts in the distribution of the population do occur (Marples 1932; Anon. 1936; Yapp 1951; Chater 1996). The low value of the Pearson correlation coefficient (-0.16), although significant, for changes within colony units between years supports this conclusion.

For the study area as a whole, changes in the number of nests were proportional to colony size, suggesting that recruitment processes were not affected by size *per se*. This finding disagrees with the hypothesis of Richardson *et al.* (1979) that an overall population increase should result from an increase mainly in the larger rookeries. This disagreement could perhaps be reconciled when the strength of the correlations are considered. The decrease is more strongly correlated across colony size than the increase (r_s = -0.41 versus 0.16 respectively). This may be due to a more even spatial distribution of losses, than occurs with the gains, across colony sites. Such a pattern might be expected where mortality generally reduces colony size across an area in a poor year, regardless of colony size, and colonies are differentially attractive, at a local scale, to recruits during a year of increase (Richardson *et al.* 1979).

The fluctuations in population size showed no obvious geographical trends. The greater increases in the west were due to the greater number of larger colonies there (compare Fig. 2.1 & 2.8). The patchy nature of the annual fluctuations suggest the causes are uneven in their operation (Yapp 1951). Locally, one colony in a cluster can increase whilst another decreases or vice versa. This may result from the movement of breeding birds between colonies (Yapp 1951). The Moran index is not sensitive enough to detect this when coupled with the overall patchiness in the population fluctuations. Movement was strongly implied in a couple of cases where very large shifts in the nest numbers of neighbouring colonies occurred in opposite directions (Fig. 2.8). This behaviour seems to be an extension of the nest moving patterns seen within rookery sites (Yapp 1951; pers. obs.). Nest maps commonly showed shifts in groups of nests within and between colony units up to 1 km away. Occasionally, larger scale movements occurred with what appeared to be whole colony shifts. In five cases, colonies recorded one year were deserted in the next, coincident with the founding of colonies of similar size, up to 4 km away. This balance between the number of colonies going extinct and those founded is recorded in the literature (Yapp 1951; Chater 1996). These movements within and between colony units and the extinction/establishment of colonies generally involve groups of less than 30 nests. This suggests the reasons for all such movements may be the same. Sometimes this is clear, as when trees within a colony are felled or the whole woodland is felled, but such a disturbance was recorded for only a few colonies. More subtle forms of disturbance such as nearby building work may be a cause, although in the majority of cases a cause could not be determined. Local agricultural changes around a colony may also cause shifts in nesting locations as individuals aggregate at a position closer to a food source in a response analogous to that proposed under the 'patch-sitting hypothesis' applied to roosts (Caccamise & Morrison 1988). In other species, movement may be caused by reduced reproductive success with recruitment to better areas (Beletsky & Orians 1991; Zicus & Hennes 1991). The proposed movement of breeding Rooks within and among colony units could be clarified by marking individuals.

2.8 Summary

Nest numbers increase at colony sites during the breeding season and so only those counts made within the asymptote period can be compared. This was assessed quantitatively in 1996 and qualitatively in 1995 and 1997, with little change occurring after 9 April until the end of the month in all years. There was little evidence of colony spacing related to colony size. Colonies were aggregated when considering distances up to 500 m around each colony, with no pattern of aggregation at larger distances. The largest colonies were found in the west near the altitudinal limit of the distribution. Nest number increases or decreases were proportional to colony size and thus the largest changes occurred in the west. The hypothesised local movement of breeding birds between breeding seasons and other behavioural interactions observed during a breeding season, mainly occurred over distances concurrent with the scale of colony clustering. Thus, it seems reasonable to analyse patterns of Rook distribution based on colony units defined by a 500 m separation.

Chapter 3

3 Verification of the ITE Land Cover Map used to delineate Rook habitat

3.1 Aims

- Outline the processes by which satellite-derived habitat classifications are produced, and describe the characteristics of the ITE Land Cover Map to be used in this thesis.
- Variation in the timing of agricultural activities may produce local errors in a classification map produced for the whole of the UK, and so field and woodland types will be compared to ground reference and aerial photo data collected for a test area.
- The ability of the ITE data to depict field and woodland types (rookery woods in particular), will be assessed.

3.2 Introduction

Rooks nest in colonies of varying sizes, spaced at irregular intervals across the landscape (Chapter 2). To model this variation in the distribution and abundance of the breeding population in relation to land use, a commercially available satellite-derived habitat classification was used. Prior to its use, it was thought necessary to quantify any errors in its representation of Rook foraging and nesting habitat. This chapter will introduce the theory of modelling breeding bird species in general, and the use of GIS and satellite imagery in this area of research. The production of habitat maps from satellite images, the terminology and the properties of the map used will then be detailed.

3.2.1 Components of bird distribution models

Multivariate techniques are used to select sets of landscape variables related to breeding bird distribution, nesting and foraging habitat requirements. Models are constructed by relating species' distribution data to the values of variables in areas likely to be utilised by the species during the breeding season (Lyon 1983; Gibbs *et al.* 1987; Andries *et al.* 1994; Austin *et al.* 1996; Bustamante 1997). Nesting habitat may be characterised by measures of the foraging habitat and assumed to be contained within it (Lyon 1983; Palmeirim 1988; Avery & Haines-Young 1990; Andries *et al.* 1994; Fielding & Haworth 1995; Bustamante 1997). Alternatively, it may be modelled separately if it is distinct from the foraging habitat (Austin 1992; Thomas 1993; Fielding & Haworth 1995; Austin *et al.* 1996). The spatially explicit analysis capabilities of a GIS are ideal for measuring these species/habitat associations, especially where the availability of suitable nesting and foraging habitat need to coincide.

The geometric characteristics of the landscape variables entered into a GIS and used for model building influence the likely source of the data. Linear features such as rivers, or roads and point features such as buildings (if not part of an urban area) are usually digitised from published maps as their resolution is too fine to be captured consistently using remote methods. Contours may also be digitised and used to categorise habitat into altitude bands (Fielding & Haworth 1995), or to derive other topographic measures such as aspect and slope by digital terrain modelling (Pereira & Itami 1991; Austin *et al.* 1996). Habitat patches can be digitised from maps (Gibbs *et al.* 1987; Bustamante 1997), although for large areas they are more commonly derived from remote survey techniques such as aerial photography (Fielding

& Haworth 1995) or satellite imagery (Lyon 1983; Palmeirim 1988; Avery & Haines-Young 1990; Andries *et al.* 1994; Austin *et al.* 1996). Within a GIS, calculations of habitat areas, boundary lengths or other measures of patch shape, and the spatial relationship between patches, can be used for model building (Palmeirim 1988; Austin *et al.* 1996). The species' spacing behaviour (Thomas 1993) or the likely area over which it can see (Andries *et al.* 1994), may also be taken into account.

3.2.2 Production of habitat maps from satellite imagery

The following description of classification procedures and terminology is adapted from Lillesand & Kiefer (1979) and Sabins (1987).

Habitat maps are usually derived from digital satellite imagery using supervised or unsupervised techniques on a computer. With supervised procedures, representative habitat types are identified in the field and digitally mapped onto the image, using processing software. The classification process extrapolates from these training data to identify all other pixels in the image with statistically similar spectral characteristics. Unsupervised classifications use algorithms to identify separable groups in the image initially, based on pixel characteristics, and these are then identified in the field. The habitat data collected to test the consistency of these classifications are known as ground reference data. Depending on the performance of the classifications, and the hypothesised requirements of the species in question, habitat types may then be merged or further sub-divided in an iterative process to give closer agreement between satellite and field based maps.

3.2.3 Description of the ITE data set

The following description is adapted from Fuller *et al.* (1994), which gives full details of the techniques and procedures used.

The Land Cover Map of Great Britain was produced by the Institute of Terrestrial Ecology (ITE) using supervised maximum-likelihood classifications of Landsat Thematic Mapper (TM) satellite image data. The baseline date for images was 1990 ± 2 years to allow for shortages. Combined summer and winter scenes for TM wavelength bands 3,4 and 5 were used to separate vegetation types and other land uses. The scenes were geometrically registered to the British National Grid (BNG) using control points on 1:50000 scale Ordnance Survey (OS) maps and combined to give a single image which was resampled from 30 m to 25 m output pixels. Typically, 70 to 80 spectral subclasses per scene were defined in training and later aggregated through an iterative classification process to give 26 target cover classes (summarised in Table 3.1). Digital masks were used to correct misclassification errors within urban areas and between coastal and terrestrial, and upland and lowland cover types. The data were then simplified by "filtering" which removed isolated pixels. Reference data were obtained by field survey of a stratified sample of BNG 1 km squares during the 1990 Countryside Survey. The spatial details were recorded on OS 1:10000 scale maps supplemented with vegetation outlines interpreted from aerial photos. The maps were digitised and converted to pixel format for 143 squares within a GIS. Field classes were aggregated to give cover types corresponding, as far as possible, to those used in the Landsat mapping. These ground reference data were compared, pixel-by-pixel, with the Land Cover Map (for full details see Fuller *et al.* 1994).

3.3 Study area

This chapter utilises data collected across two study areas. Firstly, rookery data were collected and entered into the GIS as described in Chapter 2. Secondly, a smaller area of mixed farmland (approximately 90 km^2 extending up to 13 km to the west of Durham City, UK), containing field types seen across most of County Durham was selected for the collection of ground reference data. The smaller study area was chosen subjectively, to be near roads, as is common practice (Warren *et al.* 1990), and was surveyed from 6/6/95 to 19/6/95.

Table 3.1 Summary description of the 26 target cover types (with codes) identified by the ITE in the Land Cover Map classification of the UK (adapted from Anon. 1993).

Target Class (code number)	Description
Sea/Estuary (1)	Open sea, coastal waters and estuaries
Inland Water (2)	Inland fresh water bodies such as lochs and reservoirs
Beach and Coastal Bare (3)	Mud, silt, sand, shingle, rocks and cliffs in the intertidal zone and above the tide-line
Saltmarsh (4)	Intertidal plant communities of seaweeds or halophytic grasses
Grass Heath (5)	Coastal dunes and marginal grasslands with *Festuca Ovina*, *Agrostis* spp. and *Deschampsia flexuosa* typical
Moorland Grass (9)	Upland swards of *Nardus stricta*, *Molinia caerulea*, with *F. ovina*, *Deschampsia caespitosa*, and *Juncus* spp.
Mown/Grazed Turf (6)	Grasslands mown for amenity or managed as swards through fertilising and reseeding with *Lolium perenne* for livestock grazing
Meadow/Verge/Semi-natural (7)	Grasslands managed at a lesser intensity than the 'mown/grazed' class including some hay meadows which not improved by herbicide to remove broadleaved 'weeds' or seeded with *L. perenne*
Ruderal Weed (19)	Bare ground colonised by annual and short-lived perennials including set-aside
Felled Forest (23)	Recently felled forest, usually with large quantities of brush-wood, recolonised with herbs and grasses
Rough/Marsh Grass (8)	Lowland herbaceous vegetation of fens, marshes, upper saltmarshes, and rough or derelict ground
Open Shrub Heath (25)	Lowland heath dwarf shrub/grass mixtures
Open Shrub Moor (10)	Upland dwarf shrub/grass moorland of marginal hill grazing land and areas of moor-burning
Dense Shrub Heath (13)	Lowland evergreen dwarf shrub dominated heathland with *Calluna vulgaris* and *Erica* spp.
Dense Shrub Moor (11)	Upland evergreen dwarf shrub dominated moorland with *C. vulgaris*, *Erica* spp. and *Vaccinium* spp.
Bracken (12)	Vegetation dominated by *Pteridium aquilinum*
Scrub/Orchard (14)	Deciduous orchards and areas of *Salix* spp., *Crataegus monogyna*, *Rubus fruticosus* agg. scrub and saplings or small trees
Deciduous Woodland (15)	Deciduous broadleaved and mixed woodlands
Coniferous Woodland (16)	Conifers such as *Larix* spp. and broadleaved evergreen trees
Lowland Bog (24)	Lowland herbaceous wetlands with permanent or temporary standing water
Upland Bog (17)	Upland herbaceous wetlands with permanent or temporary standing water
Tilled Land (18)	Land under annual tillage, including grass leys in their first year plus other seasonally or temporarily bare ground
Suburban/Rural Development (20)	Suburban and rural developed land with some cover of permanent vegetation
Continuous Urban (21)	Industrial, urban and any other developments, lacking permanent vegetation
Inland Bare Ground (22)	Inland ground bare of vegetation such as surfaces of rock, sand, gravel or soil, often not natural in origin
Unclassified (0)	Areas of cloud cover or of an unusual cover type not defined by the classifier training exercise

3.4 Methods

The procedures given in this section apply to the collection of information on field type and to woodland test data only, and not to the rookery data set.

3.4.1 Classification of agricultural field types

Agricultural field types were classified into one of five classes (as shown in Table 3.2). Other landscape components little used by Rooks were not surveyed. The agricultural divisions were based on those of the Land Cover Map and a knowledge of the sward types used by Rooks (Feare 1978). Pastures were recorded subjectively as being one of three main types – grazed turf, cut pasture and meadow - to allow for later recombination to test how they are represented by the ITE map. The age of the grass leys was unknown and so none were recorded in the tilled land category. Set-aside fields were recorded separately to test whether they were classified as tilled land by the ITE map.

Table 3.2 Summary description of the field types identified in the study area.

Class type	Description
Grazed Turf	Short turf of less than 10 cm, often grazed by sheep, cattle or horses
Cut Pasture	Improved pastures of *Lolium perenne* and *Trifolium* spp. cut for silage and sometimes aftermath grazed
Meadow	Rough pastures growing higher than 10 cm containing patches of broadleaf herbs, with some cattle and horse grazing, perhaps cut later in the year
Tilled Land	*Triticum aestivum*, *Hordeum vulgare*, *Avena sativa*, *or Brassica napus* monocultures, plus scattered fields of *Solanum tuberosum*, *Brassica* sp. or *Lathyrus* sp. and unplanted tilled land
Set-aside	Patchy vegetation of broadleaf herbs with scattered patches of remnant crop species, often with bare ground and treated with herbicide

3.4.2 Fieldwork protocol

The area was surveyed using binoculars from roadsides, footpaths and high vantage points. Field types were recorded onto OS 1:25000 scale maps. All fields were approached within 500 m. The classification of tilled land types was often simple, as wheat appeared dark green, barley light green and oats blue-green. The classification of pastures was more problematic because of complex patterns of management. If uncut during the survey period, a subjective decision had to be made as to whether a field with a sward height of more than 10 cm was likely to be used for silage production or was an area of rough grassland. This decision was based on the amount of herbaceous species present and the density and uniformity of the sward.

3.4.3 Establishing the test area data base in the GIS

Ordnance Survey digital Landline data were obtained, by permission from Durham County Council, for the whole of County Durham in National Transfer File format. These data were separated, using control files created in Arc/Info, into vector coverages for all the major linear features in the landscape. These included paths, roads, railways, rivers, building outlines, fence/hedge lines, and lines depicting the limits of certain vegetation types at a 1:10000 scale. The coverages were combined because, for example, a field outline may be defined by a woodland edge, a river bank and fences. The area *per se* is not digitised by the OS. The coverage was then 'cleaned' using a 7 m tolerance to remove gaps in fences caused by gates and digitising errors. It was then "built" as a polygon coverage so that fields and woodlands were recognised as distinct areas by the GIS. In Arc/Info, woodland polygons were identified and classified as a coniferous or deciduous type by overlaying two point coverages (one for coniferous and one for deciduous) extracted from the OS data. Woodlands were classified as mixed where the two point types occurred in a single polygon. The woodland coverage and the field coverage were then "clipped" using a polygon outline of the test area. Field polygons were assigned labels according to the class type recorded in the test area. Using digitised masks, large urban areas were removed from the ground reference coverage to reduce the size of the data set. Also any further errors were removed manually and some borders were added where two classes occurred in a single field.

3.4.4 Interpretation of aerial photographs

Field and woodland maps for the test area were printed out at a 1:10000 scale for comparison with aerial photographs of 1:10000 scale held by Durham County Council. The photographs were taken in August 1990 (covering the western part of the area) and May 1992 (covering the central and eastern parts of the area).

Initially, it was hoped that these photos could be used to identify field types as the date of the photos is closer than the date of ground reference collection to that of the images used for the ITE map. However, only tilled and non-tilled field types could be identified based on, for example, the presence of tractor tracks through the crops of tilled fields, animals on pasture, or the characteristic cutting patterns of silage fields. Consistent differentiation of grassland types was not attempted as it was too difficult to interpret the photos to this level. Changes in land use types from 1990/92 to 1995 were added as a second attribute layer to the field coverage.

The photos were also used to confirm the existence, shape and type of the woodlands depicted by the OS coverage. Woodland blocks were defined by the fence lines in contiguous blocks or by a distinct separation. Three types of woodland block identified on the OS coverage were confirmed using the aerial photos by examining the uniformity of canopy texture, colour and shape. Coniferous blocks were identified as those containing *Larix* spp., *Picea* spp., and/or *Pinus* spp. Deciduous blocks were those containing *Quercus* spp., *Fagus sylvatica*, *Acer pseudoplatanus*, *Fraxinus excelsior* or *Betula* spp. Those blocks containing a mix of the above species, even if segregated, were classified as mixed blocks. Under this definition, a preliminary preparation of the test data was the changing of one OS coniferous block to a mixed definition. Other manual edits included slight alterations to the shapes of woodlands along river banks and two corrections to fields classified as woodland by the OS because the seeded polygon was not properly closed. Mixed woodland blocks identified by the OS data cannot be directly compared with those depicted by the ITE data because the ITE data classifies each of the constituent grid cells making up an area separately, whereas the OS data classifies the whole block as a single area. Therefore, if only a small portion of a wood is mixed and the rest is coniferous this may be identified as such by the ITE whereas the OS identifies the whole woodland block as mixed.

3.5 Analyses

The field and woodlands coverages were converted to a grid format of 25 m pixel size, congruent with the BNG and the ITE data set. Unlabelled polygons, and the resulting cells, were assigned a "NODATA" value.

3.5.1 Field types

The five field types were reclassified into three possible combinations of field type in three separate grids, where each class or combination class was assigned the arbitrary value of 100, 200 or 300. Each of the three grids therefore contained varying proportions of these three arbitrary values depending on the combinations of field types used. Each grid of cell values could then simply be added to the ITE grid cell values of 0-25 (see Table 3.1) on a cell-by-cell basis to give unique output cell values. The combinations tested whether Cut Pasture was more often identified as Mown/Grazed Turf or Meadow/Verge/Semi-natural, and whether Set-aside was classified as Tilled Land or Meadow/Verge/Semi-natural by the ITE data. The best combination output grid was combined with that of the changes in the two main field types as interpreted from aerial photos to take account of the date of the image used by the ITE.

3.5.2 Woodland blocks

The grid cells of the deciduous, coniferous, and mixed woodland grids were given a value of 1 where woodland was present. Thus, when multiplied by the ITE grid of cell values (0-25), the value given to woodland blocks identified by the OS data and verified by the aerial photographs could be ascertained. The output grid also showed to which woodland block separate groups of ITE cells belonged. With this identification of cells it was possible to calculate the areas of woodland blocks as represented on the OS and ITE data sets. The ITE classification of mixed woodlands was tested by multiplying the cell values of the ITE grid, on a cell-by-cell basis, by both the coniferous and deciduous grids. Referring to Table 3.1 coniferous woodland should be identified by a value of 16, whereas deciduous and mixed woodlands should have an output cell value of 15, although as stated earlier mixed OS woodlands may also have cell values of 16 if areas within them are coniferous. Misclassifications of habitat types by the ITE classification would show up as other values in the output grid.

3.5.3 Rookery woods

The rookery point coverage (from Chapter 2) was combined with "shapefiles" of the ITE deciduous and coniferous woodland grid classes produced in ArcView. A woodland polygon was assumed to have identified a rookery if it contained the point or was within 50 m of it. This distance was chosen through an iterative process of examining the woodland identified on the ITE coverage and comparing it with the OS representation. Within this distance the woodland cells identified were often a part of those blocks identified on the OS coverage which contained the rookery as mapped in the field. At larger distances of 100 m or more rookeries began to be assigned erroneously to neighbouring woodland blocks. The 50 m distance was also thought to be valid as it encompassed the area around the point over which the nests of a rookery often extended, and allowed for registration and edge cell classification inaccuracies in the ITE data.

3.6 Results

3.6.1 Field types

Summary classification matrices were produced for the 3 main combinations of ground reference classes tested against the ITE classification (Tables 3.3, 3.4 & 3.5). In all cases, closest agreement was found in the Tilled Land category where 52% of all cells corresponded between the two data sets. When Cut Pasture was included with Meadow for the ground reference data as suggested by the ITE description of the Meadow/Verge/Semi-natural category (Table 3.1) the agreement was lower (22% in Table 3.3) than when Cut Pasture was included with Grazed Turf (31% in Table 3.4). Therefore it seems likely that the Cut Pastures of County Durham are classified in the Mown/Grazed Turf category of the ITE data. The correspondence of this combination with the Mown/Grazed Turf class of the ITE data was 30% (Table 3.4) as opposed to 27% when combined with the Meadow category (Table 3.3). No cells were categorised as Set-aside in the test area by the ITE data, and so the Set-aside recorded on the ground was combined with either the Tilled Land or the Meadow category of the ground reference data. More Meadow cells corresponded between the two data sets when Set-aside was combined with the Tilled Land rather than the Meadow category of the ground reference data (31% in Table 3.4 as opposed to 27% in Table 3.5). The closest overall agreement between the three main target classes tested is shown in Table 3.4, and Figure 3.1, in terms of the number (and percentage) of 25 m cells correctly classified. The vector overlay of field margins shows the shapes are well depicted by the fine resolution ITE grid. In some cases, there appear to be patches of differing quality within fields.

Table 3.3 ITE classification of the ground reference data in which the Cut Pasture was combined with the Meadow category, and Set-aside combined with Tilled Land.

	Number of cells (% of cell total for each ground reference class)			
	ITE class			
Ground Reference	Mown/Grazed Turf	Meadow/Verge/ Semi-natural	Tilled Land	Other [a]
Grazed Turf	9019 (27)	10837 (32)	8976 (27)	4836 (14)
Cut Pasture + Meadow	10701 (29)	8170 (22)	12361 (33)	5698 (15)
Tilled Land + Set-aside	8698 (25)	3005 (8)	18420 (52)	5250 (15)

[a] Other = all other ITE target cover types combined

Table 3.4 ITE classification of the ground reference data in which the Cut Pasture was combined with the Grazed Turf category, and Set-aside combined with Tilled Land.

	Number of cells (% of cell total for each ground reference class)			
	ITE class			
Ground Reference	Mown/Grazed Turf	Meadow/Verge/ Semi-natural	Tilled Land	Other [a]
Grazed Turf + Cut Pasture	18518 (30)	16493 (26)	18725 (30)	8834 (14)
Meadow	1202 (15)	2514 (31)	2612 (33)	1700 (21)
Tilled Land + Set-aside	8698 (25)	3005 (8)	18420 (52)	5250 (15)

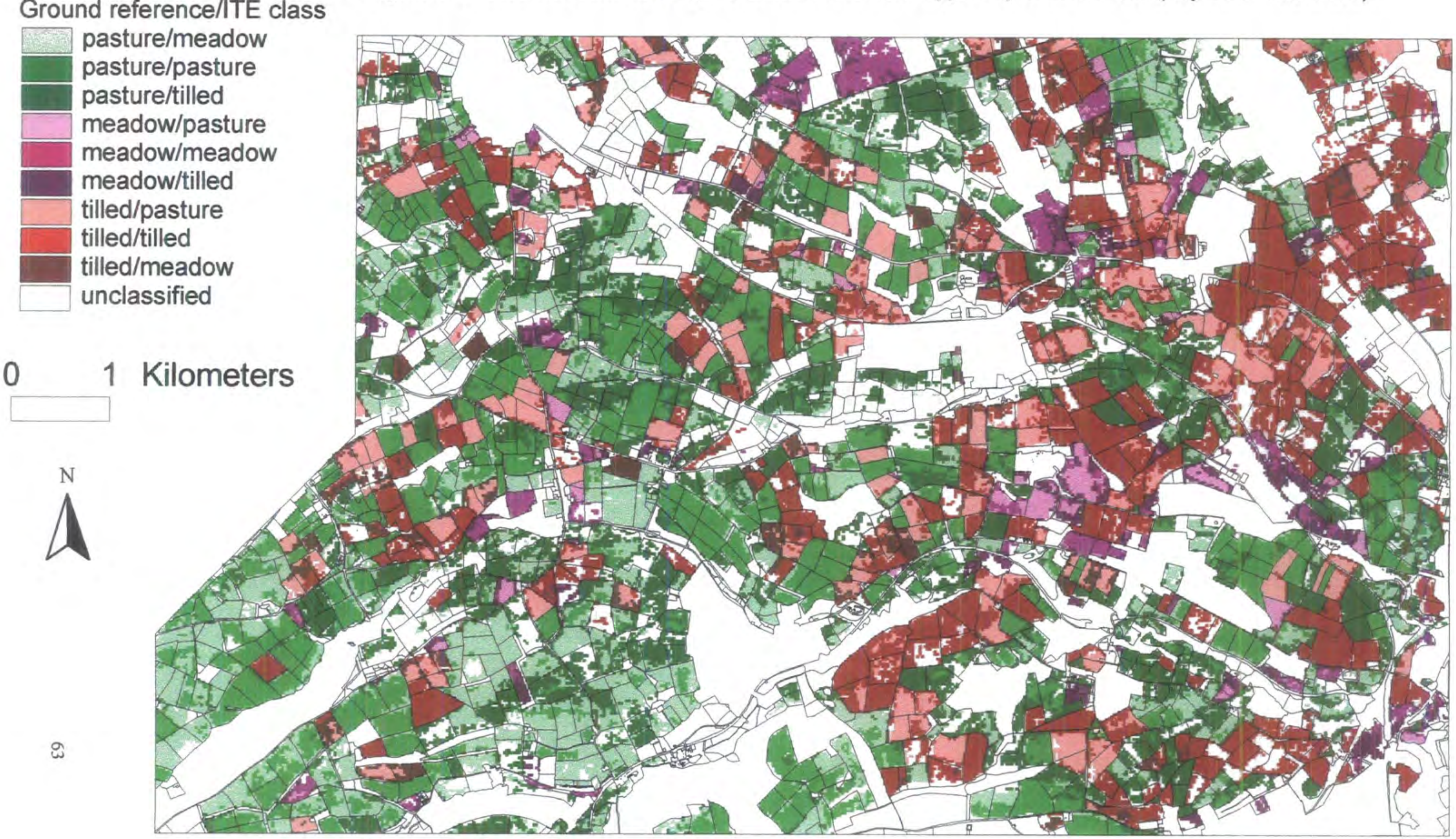
[a] Other = all other ITE target cover types combined

Table 3.5 ITE classification of the ground reference data in which Cut Pasture was combined with the Grazed Turf category, and Set-aside combined with Meadow.

	Number of cells (% of cell total for each ground reference class)			
	ITE class			
Ground Reference	Mown/Grazed Turf	Meadow/Verge/ Semi-natural	Tilled Land	Other [a]
Grazed Turf + Cut Pasture	18518 (30)	16493 (26)	18725 (30)	8834 (14)
Meadow + Set-aside	1493 (16)	2584 (27)	3459 (36)	2017 (21)
Tilled Land	8407 (25)	2935 (9)	17573 (52)	4933 (14)

[a] Other = all other ITE target cover types combined

Figure 3.1 Classification of the ground reference field types by the ITE data (key as in Table 3.6).



The classification of fields from aerial photos shows that some discrepancies between the ground reference and ITE data were due to changes in field types from the date of satellite image acquisition (1990 ± 2 years) to the fieldwork period (1995) (Table 3.6). Meadows, Cut Pastures and Grazed Turf could not readily be differentiated from each other on the photos although they could be distinguished from tilled land. Therefore these grassland classes were combined into one "Managed Grass" class (Table 3.6).

Table 3.6 Changes in field types as interpreted from 1990 and 1992 aerial photos compared to the ground reference data collected in 1995 and the ITE classification of 1990.

	Number of cells								
	Ground Reference/ITE combination [a]								
Air photo class	Pasture/ Pasture	Pasture/ Meadow	Pasture/ Tilled	Meadow/ Meadow	Meadow/ Pasture	Meadow/ Tilled	Tilled/ Tilled	Tilled/ Pasture	Tilled/ Meadow
Managed Grass [b]	0	0	0	0	0	0	611	1624	861
Tilled Land	1567	406	2199	0	66	94	0	0	0

[a] Pasture = Grazed Turf of ground reference data and Mown/Grazed Turf of ITE data
Meadow = Meadow of ground reference data and Meadow/Verge/Semi-natural of ITE data
Tilled = Tilled Land of both ground reference and ITE data
[b] Managed Grass = Grazed Turf, Cut Pasture and Meadow ground reference classes combined

For the Managed Grass category of the aerial photos, 2485 cells would have been classified as such by the ITE image. This improvement though, is countered by 611 cells which, although classified correctly in 1995, would be misclassified as Tilled Land by the ITE map when considering the air photo interpretation. Conversely, 2293 Tilled Land cells are in agreement with 2039 misclassified as Mown/Grazed Turf or Meadow/Verge/Semi-natural by the ITE map. Therefore correcting the ground reference data for date gives only slightly better correspondence with the ITE data. The summary classification (derived from Table 3.4 & 3.6) for date-corrected ground reference data compared to the ITE classification, where the Mown/Grazed Turf and Meadow/Verge/Semi-natural have been merged into a Managed Grass category, is shown in Table 3.7.

Table 3.7 Overall correspondence between the ground reference and ITE data considering the original ground reference data for 1995 and that corrected for date using aerial photos from 1990 and 1992.

	Number of cells (% of cell total for each ground reference class)		
	ITE		
Ground Reference	Managed Grass [a]	Tilled Land	Other [b]
Uncorrected			
Managed Grass [c]	38727 (55)	21337 (30)	10534 (15)
Tilled Land	11703 (33)	18420 (52)	5250 (15)
Date Corrected			
Managed Grass [c]	40601 (58)	19463 (28)	10534 (15)
Tilled Land	11449 (32)	18674 (53)	5250 (15)

[a] Managed Grass = Mown/Grazed Turf and Meadow/Verge/Semi-natural ITE classes
[b] Other = all other ITE target cover types combined
[c] Managed Grass = Grazed Turf, Cut Pasture and Meadow ground reference classes

The ground reference data, when supplemented with air photo interpretation, shows improvements of 3% and 1% for Managed Grass and Tilled Land, respectively, in its classification correspondence with the ITE data (Table 3.7).

3.6.2 Woodland blocks

All woodlands of less than 1 hectare were poorly depicted by the ITE data, whereas those above 2 hectares were represented to some extent (Table 3.8). Deciduous woodland was depicted more often by the ITE data than coniferous woodland in the same size class. This may be due to a general contrast in the shapes of these woodlands. Deciduous woodland predominated in the study area and was found along river and stream sides and in small woodland blocks. Coniferous plantings were either as large uniform blocks or as thin, linear shelter belts at field margins. For example, a conifer wood between 1 and 2 hectares not shown by the ITE data, was linear and only one pixel wide (i.e. 25 m) when gridded from the OS data, as were most of those less than 1 hectare. The spatial component of woodland representation is not shown in Table 3.8. Continuous woodland areas of the OS data were often depicted as groups of separate pixels on the ITE grid, and the sinuous and irregular shapes were often missed. Also, the edges of the woodlands were often wrongly classified by the ITE data. Thus woodland sizes were underestimated by the ITE data (Fig. 3.2 & 3.3). Larger coniferous plantings were much better represented because of their uniform character and regular shapes (Fig. 3.3). The outlier on Figure 3.3 (and in Table 3.8) was a young plantation of conifers that probably had insufficient canopy closure on the date of image acquisition to be classified as woodland by the ITE.

Table 3.8 The number of coniferous and deciduous woodlands in different size classes of the OS 1:10000 scale data set, depicted by the ITE data.

	Deciduous (Coniferous)		
Woodland area on OS (ha)	No. woodlands in each OS class	No. woodlands found on ITE	% woodlands found on ITE
≤ 1	**290** (40)	**63** (5)	**22** (13)
> 1 ≤ 2	**35** (6)	**25** (3)	**71** (50)
> 2 ≤ 3	**12** (4)	**12** (3)	**100** (75)
> 3	**17** (8)	**17** (7)	**100** (88)
All woodlands	412	135	33

Table 3.9 Correspondence between the OS and ITE classification of woodland types in terms of 25 m grid cells.

	Number of cells (% of cell total for each OS class)		
	ITE classification		
OS classification	Deciduous woodland	Coniferous woodland	Non-woodland
Deciduous woodland	790 (21)	19 (0)	3029 (79)
Coniferous woodland	96 (6)	767 (46)	809 (48)
Mixed woodland	1401 (12)	3161 (27)	7238 (61)
Non-woodland	4549	472	

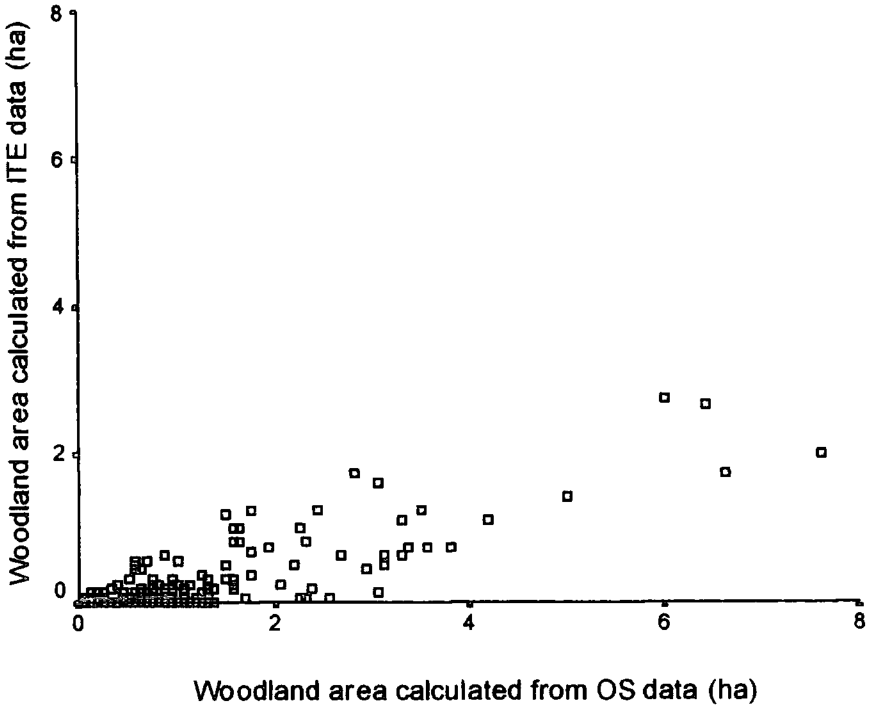


Figure 3.2 Comparison of the areas of deciduous woodland as depicted by the OS and ITE data sets.

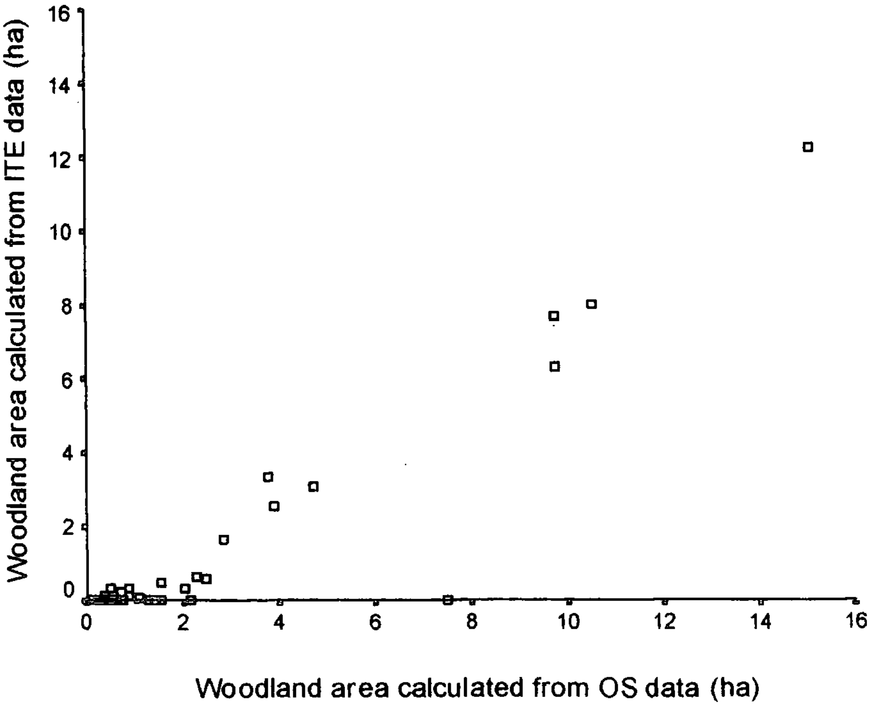


Figure 3.3 Comparison of the areas of coniferous woodland as depicted by the OS and ITE data sets.

The overall classification of woodland in the study area on a cell by cell basis shows that the ITE classification rarely confuses the two woodland types (Table 3.9). This suggests that coniferous and deciduous patches within mixed woodlands may be well represented by the ITE data. Edge pixels, small woodlands, and linear woodlands of the three OS types give rise to the large number of cells not classified as woodland by the ITE data (Table 3.9). These misclassifications are due to the spatial resolution of the original satellite image and the alignment and geometry of the feature in the landscape. These errors are less important than the classification of fields (OS class 'Non-woodland') as woodland, especially in the case of the deciduous woodland class of the ITE data, which suggests that real misclassifications have occurred (Table 3.9).

3.6.3 Rookery woods

Combining the rookery point coverage with the woodland coverages showed that out of the total of 548 rookeries, 228 were in deciduous woods, and 5 were in coniferous woods. Thus only 43% of rookeries were depicted by the ITE coverage.

3.7 Discussion

3.7.1 Field types

The ITE data set depicted the shapes of fields well and often classified them as homogenous units (Fig. 3.1). However, the quality of the field classification was poor, with confusion occurring between habitats important to this study. The errors seen in the classification matrices are due to misregistration between the data sets due to the grid cell format, and pixel mixing at the edges of habitat types. These sources of error will be higher in the dissected mosaic of habitat types typical of the agricultural landscape (Fuller *et al.* 1994). Pixel mixing is probably responsible for the different habitat types, classified by the ITE map, at field edges (Fig. 3.1). The juxtaposition of arable and pasture land with hedgerows and field borders confuse the classification algorithm. The reason for the patchy nature of more central areas in some fields is unclear, although it does suggest some changes in quality across apparently homogenous zones. This inconsistency in the ITE data is mainly confined to pastures and may have been due to patches turning muddy or being covered with straw for feed during the winter. The classification accuracy was 30% for Grazed Turf with Cut Pastures, 31% for Meadows and 52% for Tilled Land with Set-aside. This was the 'Producer's Accuracy' of how much of the ground reference data had been correctly classified rather than the 'User's Accuracy' of how much of the area had been misclassified (Story & Congalton 1986). Thus, although Tilled Land appears to be the most accurately represented it should be noted that many more cells that were not Tilled Land were assigned this classification by the ITE than was the case for Mown/Grazed Turf. The confusion between the Meadow and Grazed Turf categories was expected considering the variation in grassland management across the area. There are no fixed conventions in the division of the grassland continuum, and differences may be due to interpretation rather than real error in either data set (Fuller *et al.*, 1994). Of greater importance was the confusion of Tilled Land with Grazed Turf and Cut Pasture because Rooks select between these types (MacDonald & Whelan 1986; Chater 1996; Wilson *et al.* 1996). Some of these differences may be reconciled when it is considered that silage fields are often newly sown leys and so some may have been tilled at the time of the imagery.

When the ground reference data were corrected for the time difference between the two data sets, some improvement in the classification was seen. The date of the aerial photos does not match exactly that of the satellite imagery although it does give an idea of the likely rates of change in the landscape. These rates are not enough to explain the inconsistencies between the ground reference and ITE data sets. Using the aerial photos with the ground reference data, 58% of Managed Grass and 53% of Tilled Land was correctly classified. These values are lower than the values reported by Fuller *et al.* (1994) of 64% and 74% for Managed Grass and Tilled Land, respectively. Again, misclassifications were mainly between these two classes (Fuller *et al.* 1994). Overlaying a summer, with a winter image classification, should have helped to separate seasonally bare arable areas from permanent swards (Fuller *et al.* 1994). The planting and establishment of winter cereals may perhaps have created a more 'liberal' grouping algorithm such that some pastures were classified as Tilled Land.

The higher percentage correspondence for the Managed Grass class, hides the poor performance of the ITE data in distinguishing between sward types within this category. The use of the ground reference data, although from a different date, suggested that Cut Pastures were mainly identified in the Mown/Grazed Turf class of the ITE data rather than the Meadow class, contrary to the class descriptions (Anon. 1993 & Table 3.1). This was an important finding as these fields were used, almost to the exclusion of all others, by adults feeding their newly fledged young (pers. obs.; MacDonald & Whelan 1986). The knowledge of how this field type was classified by the ITE was therefore important to understanding the variables selected in the modelling process (Chapter 5).

Although the errors in the ITE map suggest that the correct identification of a specific field cannot be relied upon, any differences between larger areas in terms of field type totals, will represent some real relative difference. The limitations to the data could be improved upon in future studies by increasing the temporal resolution of the images used, which could be achieved by using Synthetic Aperture Radar (SAR) data (rather than TM data) as this is unaffected by cloud cover. Classifications should be made according to detailed records of ground reference data, especially in this dynamic agricultural environment.

3.7.2 Woodland blocks

Where the ITE and OS woodland maps coincided, there was consistent differentiation between the pure deciduous and coniferous types. This gave confidence in its classification of mixed areas. However, a large total area of woodland was missed by the ITE and classified in non-woodland classes. Also, as with the field study matrices, the Producer's Accuracy is given and it should be noted that large areas without woodland were predicted to contain it by the ITE. Whole field areas were often classified as deciduous woodland suggesting the algorithm confused this woodland type with the characteristics of a crop or its management. This also occurred to a lesser extent with the coniferous cover type. The prediction of forestry where there was none could hinder attempts to model the breeding distribution of the Rook. These gross misclassification effects combine with the more localised effects of woodland size, edge and geometry to create large errors in the ITE data set. The errors found in the representation of woodland size compared very well with those found by Mack *et al.* (1997), although they did not investigate pure coniferous woodland. For predominantly deciduous woodlands in East Anglia the percentage of woodlands found by the Land Cover Map in <1, >1 < 2, >2 < 3, and >3 ha classes were 18, 64, 89 and 100 respectively. This compares with the 22, 71, 100, and 100% identified in these classes in the current study. These results also agree with the suggestion of Townshend (1983) that the minimum accurately mappable unit from TM data would be of the order of 3 to 5 ha. Fuller *et al.* (1994) found that in practice, features of greater than 1 ha, depending on their shape, showed clearly on the ITE map.

3.7.3 Rookery woods

When tested with the Rook data specifically, it was found that only 43% of the nesting colonies were identified, suggesting that they show a tendency to be in small woods or those with high edge to area ratios such as linear woods. It is possible that, initially, these small woods were identified by the ITE classification. However, post-classification filtering in the production of the ITE map was used to remove isolated pixels because it was thought they represented errors (Fuller *et al.* 1994).

3.8 Summary

The accuracy of the field type classification approached that reported in the literature and suggests that the ITE map will only be of use in estimating relative differences in habitat amounts across large areas. Of those habitats identified in the field (in 1995) as Mown/Grazed Turf, Meadow/Verge/Semi-natural and Tilled Land, 30%, 31% and 52% were shown as such by the ITE data, respectively. The ground reference data showed that pastures cut more frequently for silage tend to be identified in the Mown/Grazed Turf category of the ITE data rather than the Meadow/Verge/Semi-natural class. When the field types were date-corrected using aerial photos (from 1990/1992), correspondence was improved slightly, with 58% of Managed Grass and 53% of Tilled Land identified as such by the ITE data, compared to 55% and 52% for uncorrected ground reference data (reported as 64% and 74% respectively, by Fuller *et al.* 1994).

The ITE data depicted only 43% of the woodlands containing Rook colonies. The shortfalls in the ITE data set for depicting parts of, or the whole of, smaller woodlands compares well with the error rates reported in the literature. These errors, coupled with the classification of large field areas as woodland, led to a similar test of the OS data's ability to identify Rook nesting habitat, directly (Chapter 4).

Chapter 4

4 Identifying woodlands suitable for Rook colonies

4.1 Aims

- The level at which habitat suitability for nesting Rooks is to be tested will be defined.
- For future modelling, the ability of the OS woodland data to depict woodland blocks, and those containing rookeries in particular, will be compared to the performance of the ITE data reported in Chapter 3.
- Based on findings reported in the literature, the suitability of woodland blocks will be assessed in terms of their area, proximity to roads, rivers and buildings, and according to altitude, slope and aspect, and the agricultural composition of the surrounding habitat.
- The attributes of rookery woods depicted and omitted by the OS data will be compared to each other to test whether the two sets differ greatly in terms of any of the habitat parameters measured other than woodland size, so that it is clear whether the conclusions drawn from the habitat selections of Rooks in depicted woods may or may not be applied to all Rooks.
- The attributes of rookery woods depicted by the OS data will also be compared to those of an equal number of random woodlands shown on the OS data, and where selection according to one habitat variable is demonstrated, correlations with the other variables will be examined to assess its individual importance.
- Logistic regression will be used to build a model of woodland suitability, with the aim of identifying woodlands similar to those used by Rooks.

These will then be used in Chapter 5, to assess whether there are true gaps in the breeding distribution when interactions with the members of other rookeries and the foraging habitat over a larger area are taken into account.

- Where variables are identified as being of potential importance to woodland selection, they will be correlated with the actual number of nests at a colony in an exploratory analysis.

4.2 Introduction

4.2.1 Breeding habitat suitability

The suitability of a habitat for breeding birds not only depends upon the physical characteristics required of the nesting sites, but also on the availability of foraging grounds (Morris & Lemon 1983; Gibbs *et al.* 1987; Jędrzejewski *et al.* 1988; Bustamante 1997) and, especially in colonial species, on the presence of conspecifics (Patterson 1965; Patterson *et al.* 1971; Davis 1986; Podolsky & Kress 1989; Brown *et al.* 1990; Brown & Rannala 1995; Danchin & Wagner 1997; Danchin *et al.* 1998).

The suitability of woodland blocks for nesting in terms of their position within the landscape and their access to foraging resources during the breeding season will be modelled, as it was thought that the positioning of colonies would be likely to relate to local food resources. However, it should be remembered that Rooks are largely resident, and their breeding distribution may thus relate to food resources utilised outside of the breeding season. This aspect of suitability together with the possible effects of intraspecific competition will be considered in the next chapter.

4.2.2 Nest site availability within the nesting habitat

Nest sites are the finely structured spaces where nests are built. Often they form part of a more broadly defined nesting habitat, as with the arrangement of branches on a tree or of ledges and rock faces on a cliff (Andrew & Mosher 1982; Fielding & Haworth 1995). Although these terms are at two ends of a continuum of habitat measures, it is useful in many cases to distinguish between them.

Certain decisions will be made about the positioning of the nest within the habitat and these may relate directly to nest protection from predators or harsh environmental conditions (Mosher & White 1976; Beaver *et al.* 1980; Woffinden & Murphy 1983; Rich 1986; Speiser & Bosakowski 1987; Gibbs *et al.* 1987; Olsthoorn & Nelson 1990), or to access and visibility constraints on the adults (Speiser & Bosakowski 1987; Gibbs *et al.* 1987; Jędrzejewski *et al.* 1988). Where habitat measures taken at nest sites have been compared to those taken from random locations, selection along one or more habitat gradients has often been demonstrated (Andrew & Mosher 1982; Morris & Lemon 1983; Rich 1986; Speiser & Bosakowski 1987; Jędrzejewski *et al.* 1988; Olsthoorn & Nelson 1990). The outcome of these studies though, and the apparent strength of selection, depends upon the habitat type from which the random sites are selected. Within subjectively selected nesting habitat the studies demonstrate preferences, and suggest that suitable sites remain unoccupied (Andrew & Mosher 1982; Morris & Lemon 1983; Rich 1986; Speiser & Bosakowski 1987; Jędrzejewski *et al.* 1988; Thomas 1993), even in species that are strongly aggregated (Wiklund 1982; Gibbs *et al.* 1987; Møller 1987; Olsthoorn & Nelson 1990; Clode 1993; Danchin &

Wagner 1997). Therefore, although objective measurement is the ideal (Olsthoorn & Nelson 1990), subjective assessments of suitable nesting habitat have proved very successful in identifying suitable nest sites.

4.2.3 Nest habitat selection

This chapter will not measure the factors affecting nest site selection within the nesting habitat. Instead, where a distinct nesting habitat can be identified, it will be assumed to contain suitable nest sites (Austin 1992; Thomas 1993; Fielding & Haworth 1995; Austin *et al.* 1996). Choice of nest site in relation to landscape variables and foraging grounds will be assumed to be exhibited through the nesting habitat. Therefore, in a procedure analogous to that used in studies of nest site selection, the properties of used and unused nesting habitat will be compared (Gibbs *et al.* 1987). This will test whether the habitat used for breeding is a selected subset of that available, that can be characterised in terms of its size, or position within the landscape (Gibbs *et al.* 1987; Austin 1992; Thomas 1993; Austin *et al.* 1996). These measures will be derived from Ordnance Survey (OS) data (Austin 1992; Thomas 1993; Fielding & Haworth 1995).

4.2.4 Nest habitat selection in Rooks

The woodland nesting habitat of the Rook remains unused in many areas and is not thought to limit colony size or distribution (Lloyd 1939; Patterson *et al.* 1971). Suitability may depend on woodland shape and size (Lloyd 1939; Chater 1996), or position with respect to altitude, aspect and slope, or proximity to towns, roads, rivers or changes in geology (Nicholson &

Nicholson 1930; Wynne 1932; Alexander 1933; Yapp 1934; Cramp & Ward 1936; Lloyd 1939; Williamson & Cowin 1940; Chater 1996). These findings are often subjective impressions that are not rigorously tested. Instead, the area of habitat in proximity to a feature such as a river or road may be expressed as a percentage of the whole study area and compared to the percentage of the Rook population it contains (Lloyd 1939; Chater 1996). Also, contingency table analysis may be used to assess the conservatism of nest habitat choice between years where rookeries are mobile (Chater 1996). The weakness of both methods though, is that they do not take account of the underlying distribution of available woodland (Chater 1996). The interrelation of landscape variables means that their separate effects are difficult to establish (Speiser & Bosakowski 1987). For example, with increasing altitude, changes in agriculture, the number of woodlands and climatic variables occur together, and a lack of Rooks cannot be attributed to a single causal factor (Williamson & Cowin 1940).

The proximity of rookeries to towns may be related to predation pressure in terms of shooting avoidance (Lloyd 1939). Proximity to roads may also be important in this respect, although both may provide scavenging opportunities. Although untested statistically, Rooks may show a preference for nesting near water, perhaps because of the feeding opportunities, whether these be on the exposed mudflats of estuaries (Wynne 1932) or the rich grassland bordering rivers (Roebuck 1933; Williamson & Cowin 1940). Similarly, the effects of geology are thought to act through the soils and land use of an area, which affect the Rook's food sources (Nicholson & Nicholson 1930; Wynne 1932). Therefore, it is difficult to develop the distinction made above (section 4.2.1) between variables relating strictly to the nesting habitat itself and those influencing the breeding distribution through foraging opportunities. Foraging requirements are most likely to act on site selection over the distance used during the breeding season. Site attractiveness should increase with decreased flight costs to provision the female and/or nestlings (Gibbs 1991). Therefore typical agricultural foraging habitats within 1 to 2 km of the colony may be an important constituent of site suitability (Coombs 1961; Patterson *et al.* 1971; Feare *et al.* 1974; MacDonald & Whelan 1986; Barnes 1997).

4.3 Study area

The study area was the same as that described in Chapter 2 (Fig. 2.1), except that the Tyne and Wear and Cleveland areas were omitted due to a lack of digital data.

4.4 Methods

4.4.1 Rookery data

The point coverage produced in Chapter 2 is used in the analysis. It is assumed that each point results from an independent selection of a colony site. Only those rookeries (n = 461) falling within the geographical extent of the OS digital data are considered further. The rookery definition of a 50 m separation was maintained, as this spatial grain for distinguishing rookeries was approximately the same as that of woodland fragmentation on the OS 1:10000 scale data. If rookeries beyond this distance apart had been merged and located to a central point, positional information would have been lost.

4.4.2 Woodland data

The deciduous and coniferous OS 1:10000 scale woodland coverages created in Chapter 3, were edited so that woodlands blocks divided by internal fence lines, were merged. To do this, the woodland polygons were built as line coverages in Arc/Info. This gives each line a left and right polygon identifier, with the area outside the polygons equalling zero. Lines with both sides greater than zero could now be selected in Arcedit and deleted. The label point in each woodland polygon block was then centralised. Thus woodland blocks were now defined by a gap of any size depicted by the OS data.

4.4.3 Landscape features

The OS digital 1:10000 scale line coverages of water features (including lakes, rivers and minor streams), roads (including 'M', 'A', 'B' and 'white' roads) and building outlines produced in Chapter 3 were used for the analyses. Bartholomew's digital 1:250000 scale contour data were used to create a digital terrain model (DTM) in Arc/Info for the derivation of altitude, slope and aspect grids. Altitudes modelled on the DTM were closely correlated with those read from 1:25000 scale maps, and so the DTM was thought to be adequate for the analysis. Land use types were obtained directly from the ITE 25 m cell size Land Cover Map, detailed in Chapter 3.

4.5 Analyses

4.5.1 Depiction of rookeries by the OS woodland data

Using ArcView, the rookery point data were overlaid onto the deciduous, coniferous and mixed woodland coverages, and those points falling within a woodland block were selected. Where rookeries remained unselected, they were examined manually to see if this was due to a positional inaccuracy of the rookery point. In a few cases, after consultation of field sketches and OS 1:25000 scale maps, a point was moved. The percentage classification accuracy of rookery woodlands by the OS data was calculated. The woodland type - deciduous, coniferous or mixed - was also compared with the type recorded for the rookery in the field.

4.5.2 Differences between rookeries shown and omitted by the OS data

In Arc/Info, the distance of the 461 rookery points to the line features of the roads, rivers and buildings coverages were calculated. The altitude of each rookery was obtained by overlaying the points on the DTM. The calculation of slope values for the rookeries showed that most were on relatively flat ground (<5°) and only 4% were on slopes approaching 10°. Therefore, aspect could not be calculated in most cases, and along with slope, was thought to have no influence on Rook site choice at this spatial grain. Also, the height of the canopy often meant that a rookery was above a hillside and so the nests actually had no aspect preference, and the variation in tree height would often remove slope effects. Therefore, these variables were not considered further due to the small sample sizes and the problems of definition. They also appeared to have little relevance in the field, although it is acknowledged that topography may affect local wind flow and that Rooks may make subtle distinctions between "suitable" breeding locations.

Using a program written in Arc/Info, each rooery point was selected in turn, and the three predominant agricultural ITE Land Cover types (Mown/Grazed Turf, Meadow/Verge/Semi-natural and Tilled Land) were summed for circular areas extending 500m, 1000m and 2000m around the points. The land use totals for each colony were then downloaded to an ASCII file and joined to the other attributes.

The direction and significance of the differences between the rookeries shown and omitted by the OS data in terms of these landscape attributes, and in terms of their nest counts, were compared by calculating medians and Two-Sample Kolmogorov-Smirnov Tests (K-S Test), respectively.

4.5.3 Differences between rookeries and other woods on the OS data

In a procedure analogous to that used for the rookery points, the distances from the polygon label points for all woodland blocks shown on the OS data to the linear features of the roads, rivers and buildings coverages were calculated. These measures, along with the areas for the 10662 woodland blocks, were downloaded to SPSS. From this set, one random, unstratified sample equal in size to the number of rookery woods depicted by the OS data was selected in SPSS. This subset was used in Arc/Info, where the surrounding land use totals for a central point in each woodland block were calculated using the program described in section 4.5.2. This random sample was used for comparison with the values of these variables calculated for the rookery data. The areas of the rookery woodlands were obtained in ArcView by using the rookery points to select woodland blocks from the OS woodland coverages. The areas were then downloaded and added to the attributes obtained in section 4.5.2. The two sets of woodland data are termed the "random" and "rookery" sets.

The direction and significance of differences between the rookery woodlands and the random set in terms of their areas and the other landscape attributes were calculated using medians and K-S Tests, respectively. The direction of selection for a variable was compared to the direction of the Spearman Rank Correlation coefficients between the landscape variables calculated for the random set. This showed whether selection along one habitat dimension was due to its correlation with another.

4.5.4 Building a model of woodland suitability

All variables were entered into a forward stepwise logistic regression to model the probability of a site being suitable for a rookery. This statistical technique does not require multivariate normality and linearity among the predictors and so the variables were not transformed (Tabachnick & Fidell 1996).

4.5.5 Effect of landscape variables on rookery size

The area of a rookery woodland, its altitude, distance to a road, river, or building, and the amount of the three land use types at the three buffer distances around the colony were log or root transformed to normality or near normality. These variables were then used in Partial Correlations with colony nest numbers. Obviously it was not possible to include rookeries where the woodland was not depicted by the OS data.

4.6 Results

All median values given for land use data are expressed as the number of 25 m cells of the ITE grid, which are each equal to 625 m^2.

4.6.1 Depiction of rookeries by the OS woodland data

Out of the total set of 461 colonies within the area covered by the OS digital data, 199 colonies were depicted as deciduous woodland, 83 as mixed and 17 as coniferous. Consulting field notes collected at the rookeries, it was found that 8 of the 199 colonies identified as deciduous were mixed and 2 were coniferous. Of the 83 identified as mixed, 1 was deciduous, and of the

17 shown as coniferous, 3 were mixed. Therefore the overall classification accuracy was 95% (Table 4.1).

Mixed woodlands were predominantly deciduous and so they were combined with the deciduous category, as were the coniferous woodlands due to the small number of rookeries occurring in this type, and its confusion with other classes. They were also combined because little differentiation between these types was evident in the nest habitat selection of the Rook in the field.

Table 4.1 Correspondence between the OS and field classification of rookery woodland types.

	Number of blocks (% of cell total for each field classification)		
	OS classification		
Field classification	Deciduous woodland	Coniferous woodland	Mixed woodland
Deciduous woodland	189 (99)	0 (0)	1 (1)
Coniferous woodland	2 (13)	14 (88)	0 (0)
Mixed woodland	8 (9)	3 (3)	82(88)

Having combined the preliminary woodland categories into a single type, the number of rookeries depicted as woodland areas by the OS data was 299 out of 461, a success rate of 65%.

4.6.2 Differences between rookeries shown and omitted by the OS data

The rookeries depicted by the OS data had significantly greater nest counts (median = 34; K-S Test $D_{162,299} = 3.283$, $P < 0.001$) than those rookeries that were not shown (median = 12). Figure 4.1 compares the histograms for the two sets of rookeries, and shows that there is considerable overlap between the two nest count distributions. The maximum nest count for a rookery not shown on the OS data was 156 nests. The depicted rookery set was significantly further from buildings (median = 63 m; $D_{162,299} = 3.126$, $P < 0.001$) and roads (median = 49 m; $D_{162,299} = 1.669$, $P < 0.01$) than the set not shown on the OS data (median = 29 m and median = 35 m, respectively). The depicted rookery set also tended to be closer to rivers and streams (median = 105 m; $D_{162,299} = 1.446$, $P < 0.05$) than the set not shown (median = 157 m). There was no significant difference in altitude between the two groups ($D_{162,299} = 1.322$, $P > 0.05$).

With regard to the land use surrounding the colonies, the depicted colony set had significantly greater amounts of Mown/Grazed Turf at the 500 m, 1000 m and 2000 m buffer distances (medians = 173, 834 and 3324 cells; $D_{162,299} = 1.908$, 1.913 and 1.853, $P < 0.01$, < 0.01 and < 0.01, respectively) than the set not shown (medians = 117, 604 and 2664, respectively). The two colony sets did not differ in terms of the surrounding Meadow/Verge/Semi-natural habitat ($D_{162,299} = 0.789$, 0.340 and 0.804, $P > 0.05$, > 0.05 and > 0.05, respectively) or the amount of Tilled Land within the three distances ($D_{162,299} = 0.820$, 0.924 and 0.668, $P > 0.05$, > 0.05 and > 0.05, respectively).

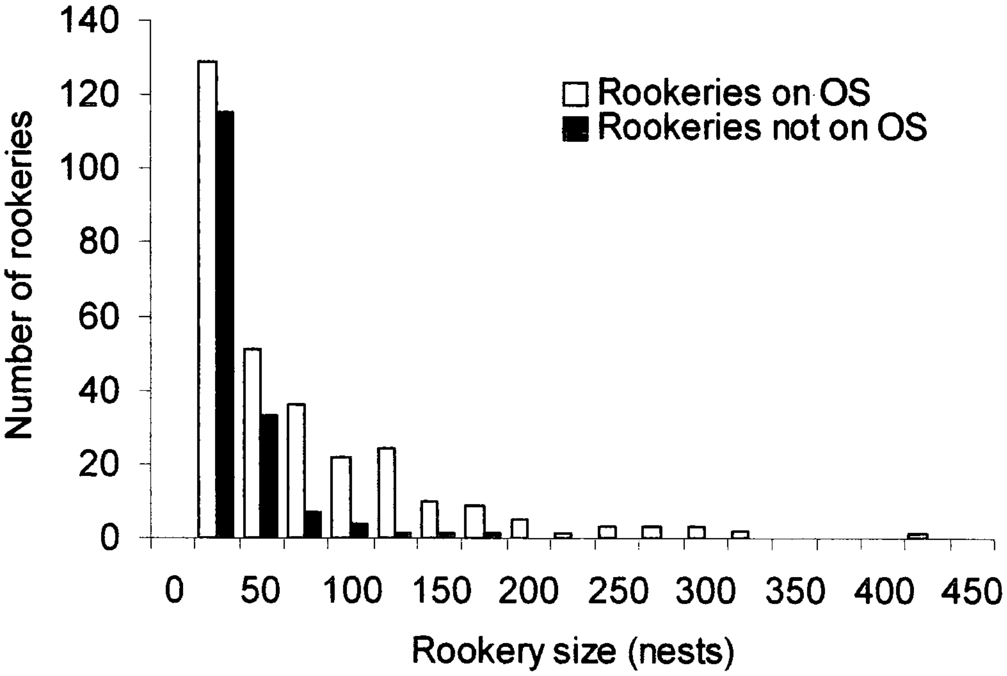


Figure 4.1 The number of rookeries in different size classes shown and omitted by the OS 1:10000 scale digital woodland data.

4.6.3 Differences between rookeries and other woods on the OS data

Where rookeries were shown on the OS data, their attributes were compared to a random sample of the same size selected from the total OS woodland set. Of the 299 random woodlands, 282 were selected from deciduous/mixed woodlands, and 17 were selected from coniferous woodlands in the total set, to make it comparable with the rookery data.

The rookery set was composed of significantly larger woodlands (median = 8880 m^2; K-S Test $D_{299,299} = 4.825$, $P < 0.001$) than the random set (median = 2777 m^2). The rookery set was also significantly closer to buildings (median = 63 m; $D_{299,299} = 1.718$, $P < 0.01$) and roads (median = 49 m; $D_{299,299} = 1.595$, $P < 0.05$) than the random set (medians = 87 m and 69 m, respectively). The two sets were not significantly different in terms of altitude ($D_{299,299} = 1.145$, $P > 0.05$) or distance to rivers and streams ($D_{299,299} = 0.654$, $P > 0.05$).

With respect to the surrounding land use, the rookery set had significantly greater amounts of Mown/Grazed Turf at the 500 m (median = 173 cells; $D_{299,299} = 2.944$, $P < 0.001$), 1000 m (median = 834 cells; $D_{299,299} = 3.599$, $P < 0.001$) and 2000 m buffer distances (median = 3324 cells; $D_{299,299} = 3.026$, $P < 0.001$) than the random set (medians = 99, 477 and 2259 cells, respectively). Similarly, the rookery set had significantly greater amounts of Tilled Land within the 500 m (median = 437; $D_{299,299} = 2.086$, $P < 0.001$), 1000 m (median = 1837; $D_{299,299} = 2.045$, $P < 0.001$) and 2000 m buffer distances (median = 7637; $D_{299,299} = 1.718$, $P < 0.01$) than the random set (medians = 374, 1589 and 6963, respectively). Also, there were greater amounts of Meadow/Verge/Semi-natural habitat surrounding rookeries than random woods, although this difference was not significant at the 500 m ($D_{299,299} = 1.186$, $P > 0.05$) and 1000 m ($D_{299,299} = 1.186$, $P > 0.05$) buffer distances, it was just significant at 2000 m (median = 3659; $D_{299,299} = 1.431$, $P < 0.05$) compared to the random set (median = 3367).

The differences in the frequency distributions of the variables between the two groups are shown in Table 4.2, with the median, maximum and minimum values for each variable.

Table 4.2 Summary statistics, with significance of differences, for all the landscape variables for the rookery and random woodland sets (n = 299 for both) identified on the OS data.

		Rookery Woodland set			Random Woodland set			K-S
Landscape variables		Median	Min	Max	Median	Min	Max	
Building distance (m)		63	2	748	87	3	701	**
Road distance (m)		49	0	768	69	2	940	*
River distance (m)		105	1	705	109	0	895	NS
Wood area (m^2)		8880	305	647518	2777	34	318892	***
Altitude (m)		110	50	400	111	44	481	NS
ITE target class	**Buffer**							
Mown/Grazed	500m	173	0	633	99	0	739	***
Turf (no. cells)	1000m	834	1	2147	477	0	2198	***
	2000m	3324	71	6885	2259	3	6490	***
Meadow/Verge/	500m	229	11	747	197	5	1119	NS
Semi-natural	1000m	926	19	2869	841	101	3794	NS
(no. cells)	2000m	3659	299	11519	3367	961	12326	*
Tilled Land	500m	437	55	1112	374	4	1165	***
(no. cells)	1000m	1837	154	4520	1589	47	3832	***
	2000m	7637	1083	17325	6963	386	14583	**

NS = not significant * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

Even where strong selection along a habitat gradient is demonstrated in Table 4.2, for example, with the Mown/Grazed Turf, it can be seen that some rookeries are still sited where none or very little is present. Similarly, some rookeries are further from buildings than random woodlands. Thus although selection has been demonstrated in the positioning of rookeries within the landscape, there are considerable 'tails' to the distribution of most variables. When the maximum rookery values for the significant landscape variables are used to select potentially suitable woodlands from the whole woodland set, 10626 out of 10662 woodlands are selected. This selection though does not consider the totals for the land use variables around all the woodlands as this is too computer intensive to calculate.

The correlations between the habitat variables across the landscape for the random selection of woodland points followed the patterns that were generally expected (Table 4.3). For example, altitude is positively correlated with the amount of pasture and meadows, and negatively correlated with arable land which is confined to the warmer and less hilly lowlands. More pasture and meadow land is found closer to streams and rivers, with tilled land found further away in better drained areas. The distance of woodlands to buildings and roads is closely correlated, with larger woodlands generally occurring further from roads and/or buildings. Larger woodlands also occur at higher altitudes, where intensive farming is less profitable, and closer to rivers and streams. This is not only due to a negative relation between altitude and distance to streams or rivers, but is also due to the larger woodlands in the valleys and denes across the region. Distances to buildings and roads are positively correlated with the amounts of pasture and meadow, probably due to the less urbanised hill pasture areas to the west of the county. These correlations follow those observed across the study area and so give confidence in the validity of the measures obtained from the GIS.

Table 4.3 Spearman Rank Correlations between all landscape variables for the random woodland set (*n* = 299).

	Spearman Rank Correlation Coefficients													
	Bd_dist	Rd_dist	Rv_dist	Wd_area	Altitude	Lu6_05k	Lu6_1k	Lu6_2k	Lu7_05k	Lu7_1k	Lu7_2k	Lu18_05k	Lu18_1k	Lu18_2k
Bd_dist	1.000													
Rd-dist	0.619**	1.000												
Rv_dist	-0.365**	-0.304**	1.000											
Wd_area	0.400**	0.311**	-0.159**	1.000										
Altitude	0.223**	0.105	-0.182**	0.131*	1.000									
Lu6_05k	0.282**	0.142*	-0.197**	0.065	0.202**	1.000								
Lu6_1k	0.251**	0.141*	-0.155**	0.070	0.227**	0.872**	1.000							
Lu6_2k	0.255**	0.184**	-0.129*	0.132*	0.247**	0.717**	0.880**	1.000						
Lu7_05k	0.280**	0.171**	-0.267**	0.088	0.566**	0.369**	0.288**	0.220**	1.000					
Lu7_1k	0.270**	0.157**	-0.230**	0.081	0.689**	0.312**	0.284**	0.236**	0.879**	1.000				
Lu7_2k	0.248**	0.137*	-0.250**	0.122*	0.771**	0.357**	0.333**	0.308**	0.754**	0.886**	1.000			
Lu18_05k	0.092	0.113	0.025	0.018	-0.438**	0.092	0.167**	0.196**	-0.394**	-0.413**	-0.409**	1.000		
Lu18_1k	0.051	0.077	0.097*	-0.024	-0.507**	0.108	0.162**	0.182**	-0.426**	-0.482**	-0.504**	0.903**	1.000	
Lu18_2k	-0.092	-0.028	0.190**	-0.104	-0.566**	0.003	0.088	0.127**	-0.501**	-0.563**	-0.619**	0.761**	0.884**	1.000

* $P < 0.05$ ** $P < 0.01$

Bd_dist = distance to a building
Rd_dist = distance to a road
Rv_dist = distance to a stream/river
Wd_area = wood area

Lu6_05k, 1k or 2k = Mown/Grazed Turf within 500m, 1000m or 2000m
Lu7_05k, 1k or 2k = Meadow/Verge/Semi-natural within 500m, 1000m or 2000m
Lu18_05k, 1k or 2k = Tilled Land within 500m, 1000m or 2000m

The directions of the significant bivariate comparisons in Tables 4.2 and 4.3 suggest that there has been selection in terms of more than one variable. Rooks seem to select in favour of larger woodlands, and for proximity to buildings or roads, as the directions of the differences between the medians for these variables go against the directions of their random correlations. According to Table 4.3, if Rooks selected larger woodlands at random in the landscape, then they should be further from urban features such as buildings and roads. This is not the case and so the results suggest that there has been independent selection of sites based on both these urban attributes and woodland size. Although the separate effects of buildings or roads cannot be assessed because of their close correlation, there is stronger selection for proximity to buildings.

Selections also do not appear to be due to sites having more of a certain land use type around them, as woodland area shows little correlation with these variables, and building and road distances tend to be positively correlated with them. Therefore if selection was in terms of land use around a woodland, the selection of areas with more of these agricultural types would result in rookeries being further from buildings and roads. This is not the case and so there seems to have been independent selection of rookery sites in terms of these land use types as well.

4.6.4 Building a model of woodland suitability

All variables were input into a forward stepwise logistic regression for model building. The model retained six habitat variables which included those identified as significant by the K-S Tests. Only land use data at the 1km buffer size were retained in the model, data for other buffer sizes were removed or remained unused, as were those identified as non-significant by the K-S Tests. The only variable retained by the model that did not have a significant K-S Test was that for Meadow/Verge/Semi-natural habitat. The regression coefficients for the variables in the model are shown in Table 4.4.

Table 4.4 The regression coefficients, and Partial Correlations (of each variable with the outcome) for the landscape variables retained by the logistic regression model derived to separate woodlands with and without rookeries.

Landscape variable (units)	Regression coefficient	Partial Correlation
Mown/Grazed Turf (no. cells)	0.0012	0.2097
Tilled Land (no. cells)	0.0009	0.1887
Road distance (m)	-0.0025	-0.0977
Wood area (m^2)	1.90×10^{-5}	0.1892
Meadow/Verge/Semi-natural (no. cells)	0.0007	0.1151
Building distance (m)	-0.0018	-0.0551
Constant	-3.0033	

The Partial Correlations of the variables with the outcome agree with the direction of the differences judged from the medians. The strongest positive association is between Mown/Grazed Turf within 1 km of a woodland and rookery presence, the strongest negative correlation is with distance from a road.

Table 4.5 Stepwise logistic regression model classification of woodlands as rookery or non-rookery groups. Classification is according to a probability cut-off value of 0.5. Both observed groups have 299 cases. The model correctly classified 71% of the overall sample.

	Predicted groups	
Observed groups	Woodlands with rookeries	Woodlands without rookeries
Woodlands with rookeries	226 (76%)	73 (24%)
Woodlands without rookeries	101 (34%)	198 (66%)

When a stepwise logistic regression was run using just those variables selected by the first stepwise procedure, it was found that the Meadow/Verge/Semi-natural variable actually reduced the accuracy of the model before the distance to buildings variable was entered (order of entry as in Table 4.4). When this meadow variable was removed from the model the distance to buildings variable was no longer entered, and three cases of correct prediction in the observed/predicted rookery category were lost. This change was very small compared to the effectiveness of the first four variables in Table 4.4 at separating the two groups.

4.6.5 Effect of landscape variables on rookery size

Woodland size was the only variable having a significant Partial Correlation with the number of nests at a colony ($Pr^2 = 0.16$, $P < 0.01$).

4.7 Discussion

4.7.1 Depiction of rookeries by the OS woodland data

The OS data had three main advantages over the ITE data in their ability to map woodland across the study area. Firstly, the overall success of the OS data in identifying observed woodland types was 95% as opposed to 93% for the ITE data. Although this suggests that the data are of similar quality, it should be remembered that the ITE data classified many non-woodland areas as woodland whereas the OS data did not (Chapter 3). Secondly, the OS data depicted the shape of woodlands more accurately than the ITE data, and consistently mapped smaller woodlands (Chapter 3). Thirdly, as a result of this second finding, the OS data identified 65% of the rookery woodlands compared to 43% for the ITE data. Therefore, the OS data were used for multivariate modelling in this, and future chapters.

4.7.2 Differences between rookeries shown and omitted by the OS data

The rookeries omitted from the OS woodland data tended to be smaller, simply because the "woodlands" not shown by the OS consist of single trees or very scattered groups along linear features such as hedgerows. Field notes made at the rookeries show this to be the case. These scattered trees often occur in urban areas and hence there is an association of these smaller rookeries with roads and buildings and with lower amounts of Mown/Grazed Turf, although the amounts of the other land use types were not significantly different.

In a preliminary analysis not detailed here, nine rookery points fell within woodland blocks depicted by another OS woodland coverage showing areas of scattered deciduous trees (as found on OS 1:25000 scale maps). These blocks were not considered in further analyses as their area bore little relation to the actual number of trees present. These rookeries were therefore considered as not having been depicted by the OS data, as they were not well delimited and so spatial information had been lost.

There were larger rookeries omitted by the OS data as shown in Figure 4.1. These tended to be in churchyards or other formal tree plantings. The ITE data did not pick out these "woodland" areas either, probably due to spectral confusion in urban areas. Large rookeries can form in just a few trees, with up to 32 nests recorded in one large Sycamore, *Acer pseudoplatanus*. Thus, it is unrealistic to expect the OS data to identify all rookeries or potential rookery sites. This could only be done by mapping all trees in an area from aerial photos. For those rookeries omitted by the OS data it would obviously be possible to compare habitat selections amongst the variables to the correlations expected at random, only if such a mapping was done.

4.7.3 Differences between rookeries and other woods on the OS data

The spatial distribution of rookery sites appears to be independently associated with several landscape variables. The logistic regression identified the amount of Mown/Grazed Turf around a woodland (or an unmeasured variable with which it is correlated) as being the most important habitat factor to be positively associated with the presence of a rookery. The 1 km distance within which this variable appears to operate on site selection is in accord with the area over which Rooks forage during the breeding season (Barnes 1997). Rooks also select sites closer to roads and buildings. The logistic regression suggests that when the correlation amongst the variables is taken into account, the distance from roads has a greater association with rookery distribution. It seems likely however that both of these variables represent an urban factor which not only gives protection from shooting and predation by some natural predators, but may also provide increased foraging opportunities (Lloyd 1939). There does not appear to have been selection for sites purely on the basis of proximity to streams or rivers in the region, but rather that this occurs where pastures and meadows are present (Roebuck 1933; Williamson & Cowin 1940).

Similarly, altitude was not associated with site selection outside of its correlation with other variables.

The positive association of woodland size with the presence of a rookery is probably due to rookeries above a certain number of nests needing woods of a certain size to provide enough nesting sites. This is supported by the results of the comparison between the rookeries shown and omitted by the OS data. The difference in nest numbers between the two sets suggested smaller rookeries tended to be in smaller woods. The Partial Correlations of the landscape variables with rookery size confirmed this association. The relationship of woodland size with rookery size is not thought to be one of cause and effect, but rather that Rooks select woodlands that can offer enough nest sites to their colony members. Personal observations of the movement of nest groups within and between woodlands across the study area over four breeding seasons, especially with the re-colonisation of sites, suggests that the sites are not limiting.

The variables most strongly associated with rookery presence can be formulated into a hierarchical theory of woodland selection. Prospecting Rooks may select an area where pastures provide good feeding opportunities for the breeding season (Feare *et al.* 1974; Purchas 1980; MacDonald & Whelan 1986). Within this area the Rooks select a woodland that can provide enough nest sites and minimises travel costs to the surrounding fields. If Rooks are persecuted in the area, those selecting woodland in proximity to buildings or roads may gain protection. Obviously this theory could be truly tested only through experimentation, as ecological inferences based on correlations should be treated with caution.

Tilled Land is the one variable that does not fit in with this theory. It was expected that this would have a negative or neutral association with rookeries, as in County Durham it is not used to any great extent during the breeding period (Barnes 1997). However, Brenchley (1984) showed that an optimal ratio of arable to pasture produces the highest densities of Rooks in 5 km squares for England as a whole, suggesting that arable land may be important in sustaining colony members outside of the breeding season. In the same study though, the amount of arable land was shown to have no effect on Rook densities in Scotland, and the same conclusion was reached by Chater (1996) for Rooks in Wales. Thus the importance of arable land to colony site selection remains unclear and may vary between locations.

The positive association with Tilled Land may also be explained by the observation that in some areas, rookeries surrounded by arable crops used waste disposal sites as the primary source of food for nestlings. Such localised effects are obviously not built into this model, and may represent a historical influence on site choice. Historical factors may also mean that some sites are not the optimal choice under the present agricultural regime, although social factors may cause them to be retained. Historical factors coupled with localised effects, such as whether or not Rooks are persecuted in an area, affect the power of the model to distinguish between sites with and without rookeries. The model will also suffer from the inaccuracies of the ITE land use classification, and the inclusion of different quality variables into a single parameter. For example, rivers, streams and ditches are all classified together as are all road types, and all types of buildings and yet some may be more important to site choice than others.

Nevertheless, the model gives an idea of the degree of suitability of a woodland, with most, if not all, woodlands being suitable to some extent considering the extreme values of the variables associated with rookeries. The model shows the attributes of woodlands preferred by Rooks, and in any given area over which Rooks have a choice of woodlands they could be expected to maximise these preferences. This choice though, will act within the constraints of other unmeasured variables not only in terms of landscape parameters but also in terms of the woodland properties themselves. For example, observations showed that where Rooks are not persecuted they are able to nest in Hawthorn (*Crataegus monogyna*) bushes, whereas, in an area where nests are shot out, they seem to have chosen the highest trees. It was also noted in hilly areas that Rooks tended to choose the parts of woodlands offering them greatest visibility. This pattern of nest placement within woodlands was often associated with the variables identified in the model, and an analysis of nest positions could be beneficial to an understanding of the importance of the individual variables.

In conclusion, Table 4.5 shows that 101 woodlands without rookeries could contain one at the 0.5 probability cut-off level. These woodlands are treated as being suitable within the confines of the variables measured. They could be true gaps in the rookery distribution or they could be unsuitable due to the competitive effects of neighbouring colonies interacting with land use over a larger area. This possibility may reduce the number of Rooks that can be supported at a site to zero, and is investigated in Chapter 5. The logistic model of the current chapter identified woodlands that are suitable for use in testing this hypothesis. The woodlands selected are a conservative sample considering the overlap of non-rookery and rookery woodland characteristics, the total number of OS woodlands available to which the model could be applied, and the sites used by Rooks not captured on the OS data.

4.8 Summary

The OS data identified 65% of rookery woodlands and correctly classified 95% of them to type – either deciduous, coniferous or mixed. Therefore, the OS woodland data were better than the ITE data at depicting the size, shape and type of rookery woodlands and woodlands in general, and were thus used for all further modelling.

Logistic regression modelling comparing the attributes of rookery woodlands shown on the OS, to a random sample, revealed that Rooks tend to utilise woodland blocks which are larger, closer to roads and buildings, and have more Mown/Grazed Turf, Tilled Land, and Meadows in the area up to about 1km away. The overlap in characteristics between the two woodland sets suggested however that when extreme variable values are taken into account virtually all OS woodlands could be suitable. However, a conservative 0.5 probability cut-off level was used to identify those woodlands most likely to be suitable. Thus, 101 unused woodlands were selected as being potentially suitable and yet unused at this relatively coarse-level of investigation.

This conclusion of possible suitability is tentative, as the potential interaction between the members of neighbouring colonies with the land use over larger areas may make woodlands unsuitable. These potential effects of competition and land use on colony counts and thus site suitability for existing rookeries will be modelled in the next chapter, and applied to these unoccupied and yet apparently suitable sites.

Chapter 5

5 Habitat and competition as determinants of Rook colony size[1]

5.1 Aims

- The relationship of Rook colony size to available foraging habitat and potential intraspecific competitors in areas of increasing radii around focal colonies will be modelled to assess the likely distance over which Rooks forage and the field types most often utilised.
- The model will then be used to predict Rook numbers for those woodland blocks identified as being potentially suitable in Chapter 4, to test whether food resource considerations or potential competitors make the sites unsuitable or if they still represent gaps in the distribution.
- The success of the model and the extent to which colony size can be explained in terms of the amount of foraging habitat and intraspecific competition for food, will be discussed in relation to the hypothesised Ideal Free Distribution of individuals across colony sites.

5.2 Introduction

The factors contributing to variation in colony size are unknown for most species of colonial nesting birds (Brown *et al.* 1990). Explanations have focused either on competitive or on habitat effects, and no studies have considered the potential interaction between the two. Assessment of the distance over which one or other of these factors influence colony size have been based on iterative correlatory approaches (e.g. Furness & Birkhead

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[1] A version of the work presented here has been submitted to *Proc. Roy. Soc. B*, as a manuscript entitled "Spatial distribution and size of Rook *Corvus frugilegus* breeding colonies is affected both by the distribution of foraging habitat and by inter-colony competition", by L.R. Griffin and C.J. Thomas.

1984; Ainley *et al.* 1995) or on observations of flight distances during the breeding season (e.g. Gibbs *et al.* 1987; Møller 1987; Bustamante 1997). The current study investigates colony size as a function of the potential interaction between the members of neighbouring colonies within a patchy foraging habitat. The distance over which this interaction is strongest is also modelled.

An ideal free (IDF) distribution results where individuals settle among suitable sites such that rewards for all individuals are equal (Cairns 1989; Brown & Rannala 1995). In addition, or alternatively, individuals may aggregate in response to social factors (Ainley *et al.* 1995; Brown & Rannala 1995; Danchin & Wagner 1997). Whilst IDF theory is under constant development (Weber 1998), it is used here in its simplest form to assume equal competitive ability between individuals (Milinski & Parker 1991). As such, an IDF distribution of individuals may be expected to lead to colony sizes which are positively correlated with the amount of suitable foraging habitat within the normal foraging range and negatively correlated with the size of neighbouring colonies if foraging ranges overlap. Social factors would result in a deviation in these relations such that colonies may attract more members than expected (Sibly 1983; Brown & Rannala 1995).

Support for the existence of IDF behavioural choices comes from the positive correlations between colony size and food resources within adult foraging ranges observed during the breeding season in, for example, Great Blue Herons (Gibbs *et al.* 1987), Barn Swallows (Møller 1987), and Lesser Kestrels *Falco naumanni* (Bustamante 1997). Also, experimental studies have shown that supplementary feeding can increase colony size in

Jackdaws *Corvus monedula* (Soler & Soler 1996). Studies showing negative correlations between the size of a colony and its neighbours also support the predictions of IDF theory, although they have been less conclusive in identifying the distance over which competition takes place. In species such as Gannets *Sula bassana*, Puffins *Fratercula arctica*, Shags *Phalacrocorax aristotelis* and Kittiwakes (Furness & Birkhead 1984), the strongest negative correlation corresponds to the maximum foraging distance during the breeding season. In others, for example, Adelie Penguins *Pygoscelis adeliae* and Gentoo Penguins *Pygoscelis papua* (Ainley *et al.* 1995), the correlations are maximised beyond this range.

The Rook is an ideal study species for assessing the interactive effects of potential extra-colony competitors and food resources on colony size. Their nests can be censused in spring to provide a good estimate of the breeding population at each colony (Brenchley 1976; Griffin in press). The location and size of colonies is fairly constant between years (Marples 1932; Anon. 1936; Yapp 1951) and unlikely to be limited to any great extent by the availability of suitable nest sites (Chapter 4; Murtland 1971; Patterson *et al.* 1971). They forage in well defined agricultural land use types throughout the year (Feare *et al.* 1974; Feare 1978; Waite 1984; MacDonald & Whelan 1986) and these can be quantified across large areas using satellite imagery. In contrast to most colonial bird species, Rooks have a strong association with their nesting rookeries throughout the year (Phillipson 1933; Coombs 1961a; Patterson *et al.* 1971) and so numbers may be related, in part, to the quantity of surrounding habitat typically used for foraging. Competition for food with species such as Jackdaws, Starlings and even Badgers *Meles*

meles could affect colony size, although Waite (1984) demonstrated little overlap in the foraging niches of sympatric British corvids. Rook colony size shows no simple negative correlation with the size of neighbouring colonies within distances over which foraging ranges overlap, and within which they are likely to compete (Marples 1932; Coombs 1961a; Patterson *et al.* 1971; MacDonald & Whelan 1986; Barnes 1997). Thus, it is hypothesised that an interaction between intraspecific extra-colony competitors and the spatial distribution of the foraging habitat influences both the size and distribution of Rook colonies. This hypothesis is tested by using a multivariate regression model incorporating these features to predict the size of colonies recorded in the study area, and that could potentially colonise the woodlands identified in Chapter 4 as being otherwise suitable.

5.3 Study area

The study area covers the contiguous survey area shown in Chapter 2 (Fig. 2.1).

5.4 Methods

5.4.1 Rookery survey data

Following the details given in Chapter 2, a sample of 18 colonies of varying size were counted every four days between 1 April and 25 April 1996. When the nest numbers reached a plateau (9 April), the remaining colonies in the study area were counted. The other colonies in the study area were located by following flight lines from winter roosts and from data collected in historical surveys (D. Sowerbutts pers. comm.). Also, most of the study area is within 2 km of a road, and so colonies could be located using binoculars within this distance. With reference to landscape features, view fields were marked on OS 1 : 25000 scale maps, delimiting the areas searched. This ensured complete survey coverage of the woodlands in the study area.

The co-ordinates of single nests or nest groups more than 50 m from any other such group were extracted from the OS 1 : 25000 scale maps and input as points into Arc/Info. Within the GIS, colonies were aggregated to a central point if less than 500 m apart to maintain positional accuracy whilst reducing computation times, giving a sample size of 308 colonies. Although this is not the definition of a rookery utilised in most studies and surveys (Sage & Nau 1963; Patterson *et al.* 1971) it does conform more closely to that postulated by Coombs (1961a) and covers the distance over which colony units were found to be clustered (Chapter 2). The members of neighbouring rookeries showed a tendency to interact when displaying at the rookeries (pers. obs.), and often had overlapping foraging ranges (Barnes 1997), over this distance of 500 m.

Nest counts were root transformed to normality for use in the parametric correlations.

5.4.2 Environmental data

Habitat data for the area were extracted by the ITE from the Land Cover Map of Great Britain. The map was produced from Landsat Thematic Mapper data for 1990 ± 2 years to give a 25 m grid of 26 cover types (Fuller *et al.* 1994).

Fourteen habitat types classified by the ITE were not present or were very localised within the study area and so would not be of use to a general model. A further nine habitat types were removed as they were unlikely to be used by Rooks for foraging. Therefore the original 26 cover types were reduced to a set of 3 that represented the majority of the agricultural mosaic: Mown/Grazed Turf (pasture); Meadow/Verge/Semi-natural (meadow) and Tilled Land.

The land use variables were either $\log_{10}$ or root transformed to normality as necessary.

5.5 Analyses

5.5.1 Calculation of the number of potential competitors

The assumptions made when modelling the number of potential competitors were that each colony extends its feeding range in a circle out to the same distance as every other colony and that birds are equally likely to forage in all parts of this range. This assumption greatly simplifies published accounts of the home range shapes of Rooks which can be much more irregular (e.g. Patterson *et al.* 1971), with concentrations of birds in preferential feeding areas. However, where suitable foraging habitat is more evenly arranged, rookeries may have roughly circular home ranges during the breeding season (Barnes 1997).

The relationship of the area of overlap of two circles to the distance between their centre points was modelled using cubic equations. Each of the foraging range sizes tested had a unique equation fitted as necessitated by the changing proportional overlap. These equations were then used to convert the actual distances between colonies observed in the study area (extracted from the GIS) to proportions of overlap for each foraging distance. This proportion was then multiplied by the number of nests at neighbouring colonies to give the number of pairs likely to encroach within the range of the focal colony. For each colony in turn, these potential competitors were summed for all the neighbouring colonies with which they overlapped considering the foraging range in question. This gave a measure of the number of potential competitors which was root transformed to normality.

5.5.2 Univariate correlations

The univariate relationships of colony nest counts to habitat availability and potential competitors were determined using Pearson Correlation coefficients (*r*). Correlations were calculated for foraging ranges encompassing those commonly reported in the literature, from 1 km (Coombs 1961a; Patterson *et al.* 1971; MacDonald & Whelan 1986; Barnes 1997) to 6 km (Purchas 1980). On this basis, of the 308 colonies in the study area, 111 could be used for the Pearson Correlations as they fell within 12 km of the set of known neighbouring colony locations (Fig. 5.1).

A program written in Arc/Info selected each colony in turn, "buffering" it at kilometre radius intervals. The resulting areas were "gridded" and overlaid onto the ITE data, and the number of 25 m grid cells of each cover type summed. The habitat data and the distances between all colonies (for the calculation of potential competitors outlined above) were downloaded into SPSS for analysis.

The values of the Pearson Correlation coefficients at each of the 1-6 km radii were plotted to assess the distance over which colony size was most strongly related to foraging habitat and potential competitors.

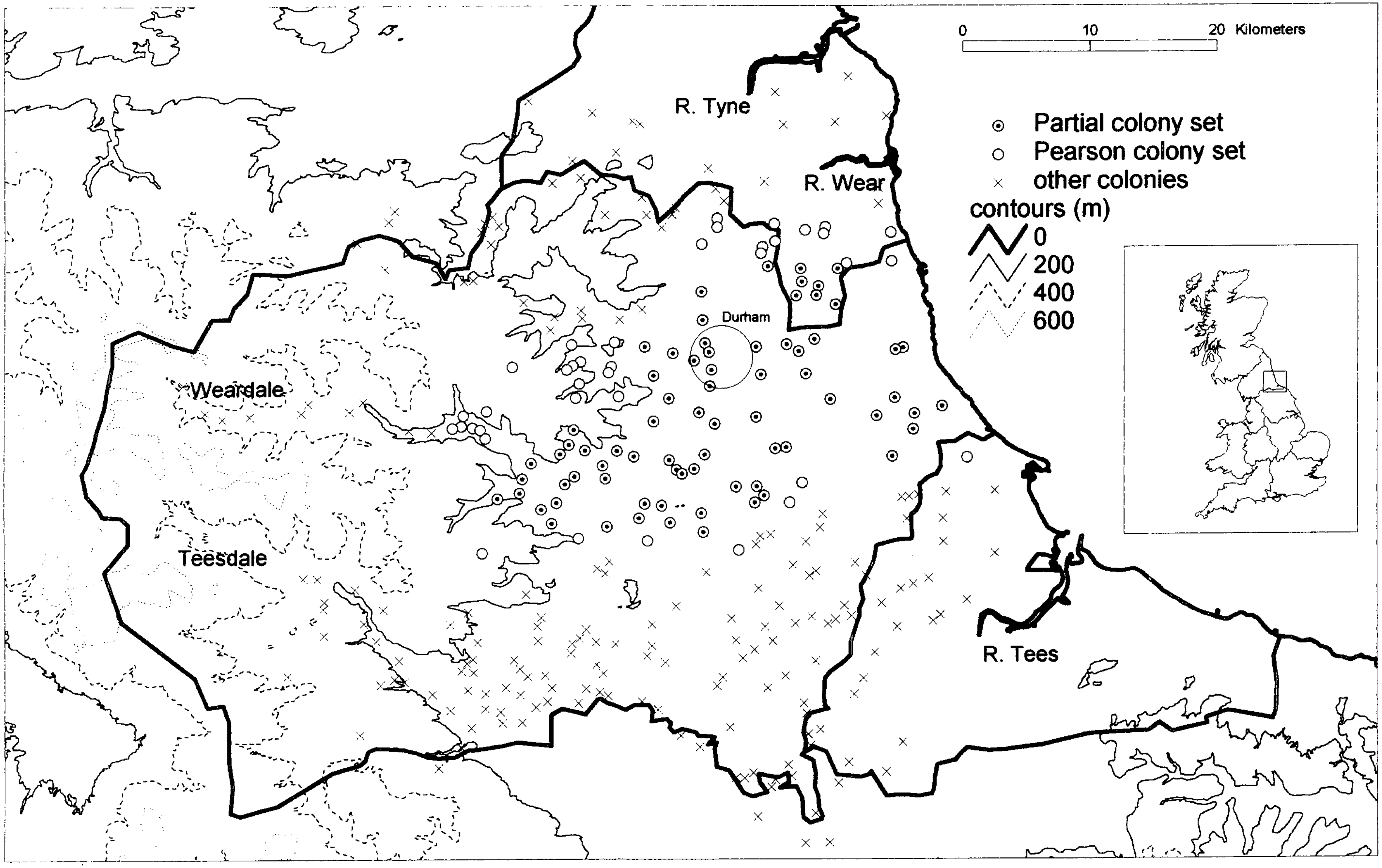
5.5.3 Partial Correlations

For comparison with the univariate approach outlined above, the direct and indirect effect of habitat on colony size was measured using Partial Correlations (Sokal & Rohlf 1997). The hypothesis tested with data extracted from the GIS was that the amount of foraging habitat affects the size of the focal colony directly, and also indirectly through the potential competitors it supports within the foraging range of the focal colony. Partial Correlations were used because foraging habitat may have positive effects, and competitors negative effects on focal colony size, with one masking the effect of the other.

The distance over which the variables most affect Rook numbers was investigated by assigning to each colony increasing circular hypothetical foraging ranges with the amount of habitat and the number of potential competitors calculated as for the Pearson Correlations.

The largest range size (8 km) was chosen through an iterative process of calculation and examination of the strength of the correlations, coupled with the need to maintain large sample sizes for subsequent model assessment. Of the 111 colonies used with the Pearson Correlations, the iterative procedures with the Partial Correlations extended the distance within which all neighbouring colonies needed to be known to 16 km and thus reduced the sample size to 73 (Fig. 5.1).

Figure 5.1 Colonies used in Pearson Correlations (n=111) and Partial Correlations/model building (n=73).



5.5.4 Validation using random simulations

Ten random simulations at each range size were used to test for the generation of spurious correlations between the nest count and habitat variables due to the method used to calculate the number of potential competitors. Within the GIS, colony counts were randomly reassigned to the colony locations recorded in the field, thus avoiding the problem of site suitability and maintaining the spacing between colonies. Potential competitors were calculated using the cubic equations derived for use with the field data. Coefficients of the Partial Correlations of the random counts with the numbers of potential competitors, and the habitat availability data from the actual colony locations, were compared with the coefficients obtained for the actual count data.

5.5.5 Multivariate model building

The significant variables for the range size at which the Partial Correlations were maximised were entered into a multiple regression. The data were examined for multivariate outliers through calculation of Mahalanobis distances and from residual scatterplots (Tabachnick & Fidell 1996). No consistent outliers were found using these methods. The sample size of 73 colonies, the response variable, with 3 predictor variables is acceptable for testing the multiple correlation (Tabachnick & Fidell 1996).

Samples were randomly assigned to one of two groups for a cross-validation procedure (Snee 1977). The model was rebuilt on one group (n = 37) and used for prediction of the dependent variable in the other (n = 36). The distribution of the residuals of the two sets were then compared using a *t*-test.

The performance of the model across the range of colony sizes was assessed by plotting the predicted colony counts against those observed in the field.

The spatial pattern of residuals was also examined to check whether there was likely to be any other geographical factors which could be added to the model to explain remaining variation (Goodchild 1986).

5.5.6 Predictions of the multivariate model

The multivariate model produced, was used to predict colony sizes for the set of woodlands identified as being otherwise suitable in Chapter 4. The amounts of the various land use types and the number of potential competitors were calculated for these woodland blocks using the methods outlined above for the actual rookery woods.

5.6 Results

5.6.1 Univariate correlations

The Pearson Correlations between colony size and numbers of potential competitors were negative at all foraging range sizes up to 6 km, but significantly so only at 2 km (Fig. 5.2). Colony size was also (non-significantly) negatively correlated with the area of tilled land, and highly positively correlated with the area of pasture within 3 km of the colony. Colony size was significantly positively correlated with the amount of meadow surrounding a colony at all the range sizes tested.

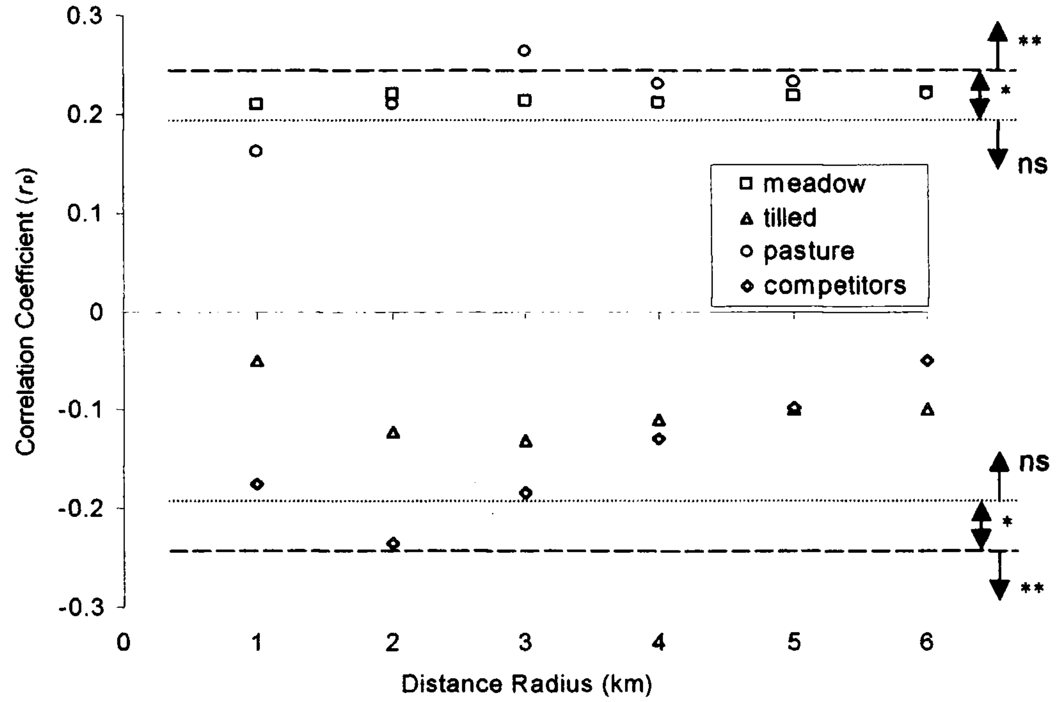


Figure 5.2 Pearson Correlations of colony size with habitat and potential competitors across the range sizes tested. * = $P < 0.05$; ** = $P < 0.01$; ns = not significant

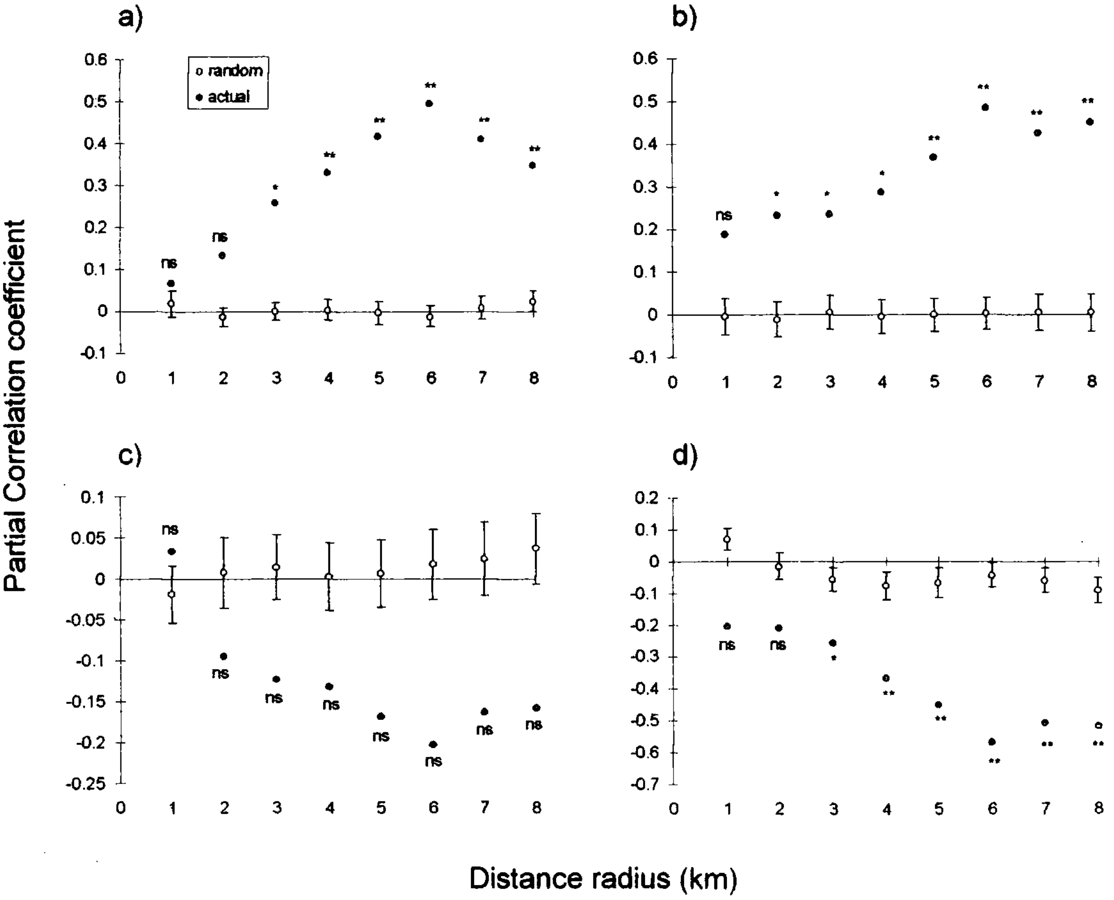


Figure 5.3 Partial Correlations of colony size with: a) pasture; b) meadow; c) tilled land; and d) potential competitors for the actual and random distributions of nest counts for the range sizes tested. * = $P < 0.05$; ** = $P < 0.01$; ns = not significant

5.6.2 Partial Correlations

Examination of the Partial Correlation coefficients show that colony size is most strongly correlated with the number of potential competitors and areas of particular types of land use within a foraging range of 6 km. The correlations with areas of pasture and meadows increased from being non-significant at lower ranges to highly significant at 6 km but then declined (Figs. 5.3a & 5.3b). As with the Pearson coefficients, nest counts were not significantly correlated with the area of tilled land (Fig. 5.3c), but were increasingly negatively correlated with numbers of potential competitors as the distance was increased from 1 to 6 km (Fig. 5.3d). The correlation of focal colony nest counts with numbers of potential competitors within 6 km was stronger than with any of the land use variables.

All random simulations for the variables across all range sizes showed no consistent trends and were not significantly different from a zero value correlation (Figs. 5.3a – 5.3d).

5.6.3 Multivariate model

The variables with the highest Partial Correlation values (i.e. at a range of 6 km) were used for model building in a multiple regression. The pasture, meadow and potential competitor variables were entered in one step. The tilled land variable was not used. The resulting overall model for the number of nests at a colony was as follows:

$$Y = -1.394x_a + 0.144x_b + 16.029x_c - 38.540$$

Where Y = the square root of the number of nests at a colony, x_a = the square root of the number of potential competitors, x_b = the square root of the amount of pasture, x_c = the $\log_{10}$ of the amount of meadows. The model gave only a moderate fit to the data ($r^2 = 0.31$ $F_{3,69} = 11.65$ $P < 0.01$). Cross-validation showed no significant differences in the distribution of residuals between test ($n = 36$) and model ($n = 37$) groups ($t_{71} = 1.025$ $P > 0.05$).

There is some tendency for the model to predict higher nest counts for smaller colonies and lower nest counts for larger ones (Fig. 5.4). This does not seem to be associated with a geographical trend as shown by the lack of pattern in the spatial positioning of the outlying group of larger colonies identified in Figure 5.4, and in the distribution of positive and negative residuals across the area as a whole (Fig. 5.5).

5.6.4 Predictions of the multivariate model

The 101 woodland blocks predicted to contain a rookery from the logistic regression in Chapter 4 were reduced to a set of 29 (27 deciduous blocks and 2 coniferous ones) in the GIS by selecting all those for which all rookeries within 12 km were known. This was an essential criterion for the calculation of the potential competitor variable in the model. The predicted sizes of colonies that could exist within these woodland blocks are shown in Figure 5.6. The results suggest that when the interaction of competitors with a patchy foraging habitat is taken into account, small new colonies could form within the centre of the existing rookery distribution, with larger colonies in the western, and perhaps eastern fringes.

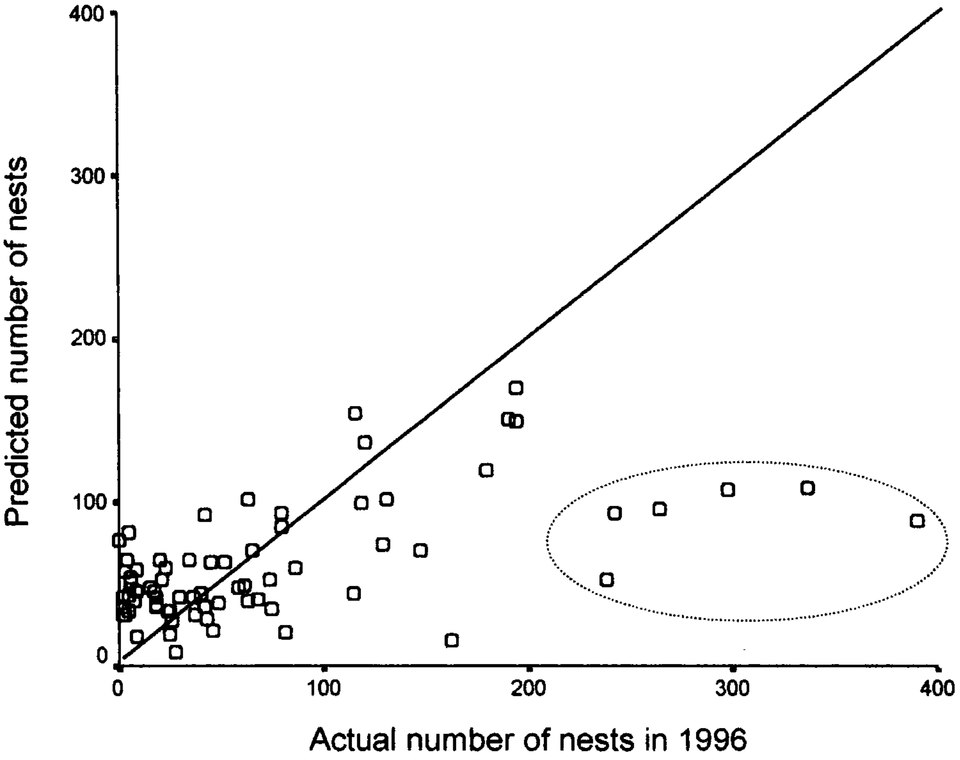


Figure 5.4 The predicted number of nests against the actual number recorded for the colonies used in the multiple regression. The straight line represents perfect prediction. The group of outliers highlighted by the oval are shown in Figure 5.5.

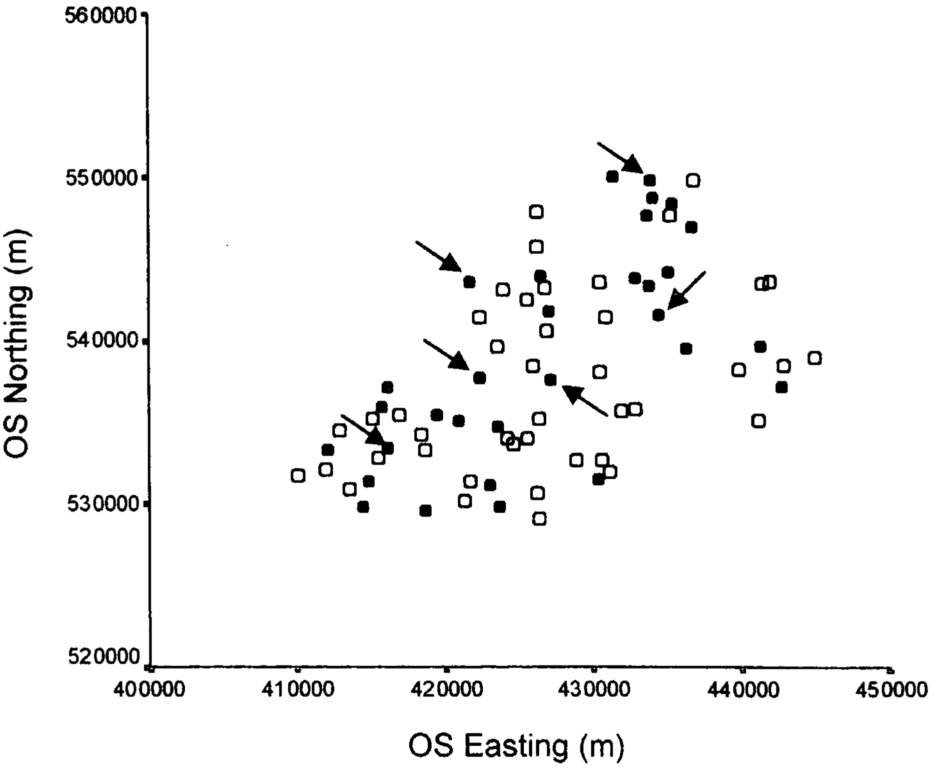
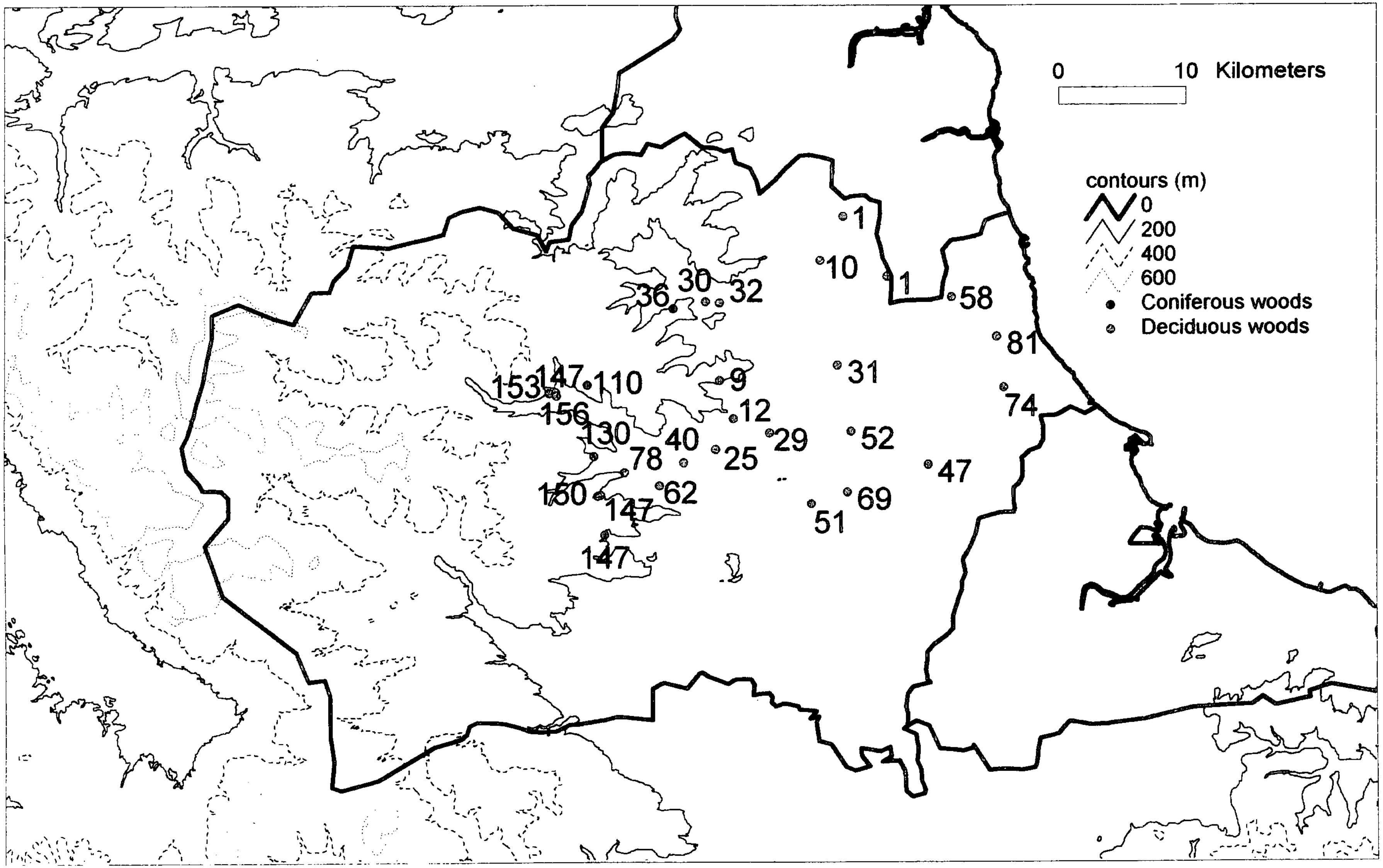


Figure 5.5 The OS grid references of the colonies show the geographical position of those colonies with positive (•) and negative residuals (○) from the multiple regression. Arrows show the colonies highlighted in Figure 5.4.

Figure 5.6 Predicted colony sizes for woodland blocks remaining unused by Rooks



5.7 Discussion

5.7.1 Relation of colony size to habitat and competitors

The simple univariate correlations suggested that colony size may be limited by the amount of pasture and meadow, and the number of Rooks from neighbouring colonies with overlapping foraging ranges within distances of 2 to 3 km. These correspond to typical flight distances of the Rook during the breeding season (Coombs 1961a; Patterson *et al.* 1971; Purchas 1980; MacDonald & Whelan 1986), suggesting a feasible system by which Rook colony sizes could be limited. However, the weakening of the Pearson Correlations over larger distances could be due to an increase in the overlap of the foraging ranges between neighbouring colonies, such that the habitat over a larger area supports the members of many colonies.

Previous studies using univariate correlations differ in their assessment of the range at which bird species relate to habitat and potential competitors. Furness & Birkhead (1984) found that the negative correlations between focal colonies and their neighbours were strongest over distances that corresponded with the normal adult foraging range during the breeding season. For polar, ocean systems Ainley *et al.* (1995) found negative correlations between focal and neighbouring colonies beyond the maximal foraging range of breeders. Therefore, they suggested larger scale metapopulation dynamics and prey depletion outside the chick provisioning periods may limit colony sizes. The conclusions reached in these previous studies may have differed because the potential effect of the spatial distribution of the food resource was not accounted for, as this could not be easily quantified over such large areas (Diamond 1978; Cairns 1992).

Instead it was assumed that prey was distributed uniformly or was superabundant (Furness & Birkhead 1984; Ainley *et al.* 1995), when even in Antarctic ocean systems this may not be the case (Kirkwood & Robertson 1997). Also, range overlap was not modelled as a function of the distance between colonies. Instead, the use of total counts was a simplification which could have weakened the correlations between focal colony nest numbers and the number of nests at neighbouring colonies (Furness & Birkhead 1984; Ainley *et al.* 1995).

The amount of foraging habitat and the number of potential competitors was modelled in the current study, and Partial Correlations tackled the problem of their interaction by holding each variable constant in turn. The results suggest that the spatial distribution of Rook colony sizes could be limited via interactions between the area of available habitat patches and the number of potential competitors over distances of 6 km. This is a dramatically different conclusion from that reached under the univariate correlations, although all correlation plots supported the *a priori* expectations of a positive relation of Rook numbers with pasture and a negative relation with competitors. More specifically, tilled land was not important, as was also found for Rooks in Wales (Chater 1996). The 6 km distance corresponds more closely to the maximal foraging ranges of Rooks during non-breeding periods (Purchas 1980). This result supports the proposal that food availability outside the chick provisioning period may limit colony size (Lack 1966; Diamond 1978; Ainley *et al.* 1995). This may occur in summer when juvenile Rook mortality is greatest (Holyoak 1967), especially during drought periods when earthworm availability may be low, and Rooks obtain a lower calorific intake, spending a high proportion of the long days foraging (Feare *et al.* 1974), with foraging ranges showing increased overlap (Patterson *et al.* 1971; MacDonald & Whelan 1986).

5.7.2 Performance of the model

The 6 km foraging range values for statistically significant variables were used to construct the multivariate regression model. The variance in colony size explained by the predictor variables was significant, although quite low (31%). This value is the same as that obtained for Lesser Kestrel colony sizes by Bustamante (1997). The variance left unexplained in the Rook model may be due to a number of factors, foremost of which may be that the Rooks do not select between colonies in accord with IDF theory. Individuals may have selected sites based on the number of conspecifics present rather than strictly upon the habitat resources available at a site, leading to larger than optimal colony sizes (Sibly 1983; Brown & Rannala 1995; Danchin & Wagner 1997). This has been suggested to occur in Cliff Swallows where there may initially be an IDF distribution of individuals amongst colony sites (Brown & Rannala 1995). Figure 5.4 supports the idea that some sort of social attraction effect operated on the spatial distribution of nests among the colonies, with larger colonies attracting more breeding pairs than expected considering the availability of foraging habitat and the number of potential competitors. When measuring relative recruitment between pairs of differently sized Rook colonies, Richardson *et al.* (1979) found that an overall population increase did correspond to an increase mainly in the larger colonies, which suggests that differential attractive effects may operate.

The predictions of the model for a subset of woodlands selected using the logistic regression in Chapter 4, showed that there were probably "gaps" in the rookery distribution whereby Rooks could be supported in newly founded colonies or at greater numbers in existing colonies (Fig. 5.6). These apparently suitable, yet unused woodlands are unlikely to be consistently different from those containing rookeries in terms of some other unmeasured variable. The subset of woodlands was also a conservative sample of the total OS woodlands available and so it seems suitable woodlands are readily available. It should be noted however, that the predictions shown are for each woodland independent of the others, such that if one site did become established another site may become untenable.

Even within the error of the multivariate model, Fig. 5.6 does suggest the central part of the colony distribution is more saturated with Rooks than the western area, and this does not appear to be due to any geographical bias in the predictions of the model (Fig. 5.5). The predictions for colony sizes in the central area suggests a possible reason for the movement of smaller rookeries alluded to in Chapter 2 and by Yapp (1951) and Chater (1996). These rookeries, which are often less than 30 nests, may be more mobile than larger colonies because they are constantly seeking these predicted gaps in the distribution. These gaps will depend on the performance of neighbouring colonies and changes in land use and so their viability will change from one year to the next, which may make colony shifts necessary.

The prediction of larger colony sizes to the west is for woodland blocks outside of the geographical extent of the colony subset used for constructing the model, and suggests its predictions may break down beyond the extent of the data set used. This may be due to geographical effects occurring in these fringe areas which could not be detected by the residual plot for the colony subset (Fig. 5.5). Such factors may include a lower density of Rooks in the west due to greater persecution in this area (I. Findlay pers. comm.) or it may be due to increased competition from juvenile birds that may disperse to upland areas after the breeding season (C. Thomas pers. comm.). These variables were not measured in the current study and, coupled with other more general problems, may affect model performance. Such problems include the measurement of the quality of colony site resources over the large area used in this study (Brown & Rannala 1985). For example, the gross vegetation categories used contain a variety of different quality habitat types in terms of their animal food content and availability (Waite 1981; Boag *et al.* 1997; Morris & Thompson III 1998). These habitat types may be more precisely correlated with Rook numbers. Also, misclassifications in the ITE Land Cover Map (26% for tilled land and 36% for "managed grassland", Fuller *et al.* 1994; Chapter 3) combined with the time lag between the collection of the habitat and bird distribution data, will reduce model accuracy. Finally, the assumptions made when calculating the number of potential competitors – because the extent of overlap between the foraging ranges of colonies was not measured in the field - may not be met. Instead, foraging ranges may be irregularly shaped, unevenly used (Patterson *et al.* 1971), or be larger for bigger colonies (MacDonald & Whelan 1986; Cairns 1989). The use of circular foraging ranges was justified on the basis of observations of colony home ranges during the breeding season (Barnes 1997). Home ranges extended to roughly the same distance for all colonies, and when unsuitable habitat was taken into account, were approximately circular. The extent to which this assumption holds outside the breeding season is less well known, although colonies often have overlapping foraging ranges and so a "hinterland model" (Cairns 1989) whereby colonies are allotted exclusive foraging areas based on proximity, was deemed inappropriate.

5.8 Summary

The multivariate model explained 31% of the variance in Rook colony nest numbers, suggesting that Rooks show a tendency towards an ideal free distribution of individuals amongst colony sites. Competition from neighbouring colony members and the availability of foraging habitat, and especially pastures, at distances up to 6 km may play a role in determining individual colony size. The current chapter shows how conclusions can be dramatically affected if the interaction between potential competitors and the patchiness of the foraging habitat is not taken into account. More specifically, Rook colony sizes may be limited outside of the breeding season when foraging ranges are larger and overlap to a greater extent, demonstrating the importance of identifying the distance over which interactions are strongest in any study.

Chapter 6

6 Spatio-temporal variation of Rook numbers in relation to habitat

6.1 Aims

- The predicted relationship of Rook numbers to certain land use types found in Chapter 5, will be verified using an independent source of data on the agricultural land use types in the study area produced by the Ministry of Agriculture, Fisheries and Food (MAFF) for 5 km grid squares.
- The MAFF data will also be used to test for a relationship of colony size to livestock variables which may indicate grazing intensity effects on the forage quality of the pastures.
- Although the spatial resolution of the MAFF data is less than that of the ITE data, the MAFF data is available over many years, and will be used with older Rook surveys to test for correlations between changes in Rook numbers and land use through time, which will again be discussed in relation to the Ideal Free Distribution.

6.2 Introduction

The abundance of Rooks in relation to land use has already been examined using one source of land use data (Chapter 5). However, it is known that there are inaccuracies within this data set which could affect the performance of the model (Chapter 3). Therefore it was thought advisable to test the predictions of the model produced in Chapter 5 against those based on another independently collected source of habitat data. The data set used was produced by the Ministry of Agriculture, Fisheries and Food (MAFF) and has been used in other studies analysing changes in Rook numbers through time (Lomas 1968; Chater 1996). However as yet, no studies have used these data to examine the spatial distribution of Rook numbers within a breeding season.

Although the MAFF data have shortcomings compared to the ITE data, especially in terms of spatial resolution, it was hoped that its finer breakdown of crop, pasture and livestock types would give a better indication of the importance of specific habitat qualities. Moreover, the ITE data provide only a snapshot of the habitat situation through time whereas the MAFF data can be obtained for many different years. The reliability of the MAFF will be assessed initially because an earlier paper recorded impossibly large changes in the areas under cultivation suggesting that errors in the recording of the data may have occurred, urging caution in its use, especially with the older parish agricultural survey data (Yapp 1951).

The current chapter will provide not only a check for some of the predictions of Chapter 5, but also an analysis of changes between years. This may give some indication as to why there have been past fluctuations in Rook numbers across the country as a whole. The loss of grassland and the use of winter sown crops have been cited as possible reasons for Rook declines (Sage & Whittington 1985).

6.3 Study area

The study area covers the contiguous survey area shown in Chapter 2 (Fig. 2.1).

6.4 Methods

6.4.1 Rookery data

The size of rookeries in the study area for 1996 was recorded following the methods given (Chapter 2; Griffin in press). Using Arc/Info, the 50 m definition rookery nest counts were summed for a 5 km cell size grid with an origin matching that of the habitat data grid. Each cell received a nest sum value for all the rookery nests it contained. The size of rookeries in the study area for 1975/76 was obtained from BTO survey records for County Durham (with permission from D. Sowerbutts). Some extra data covering the Teesdale area were also used (I. Findlay pers. comm.). The data were recorded by many different workers, with most rookeries being counted in late April/early May 1975. A small number of rookeries believed to have been missed during this survey were counted during the same period in 1976. Colonies were defined as a group of nests 100 m or more from any other such group (Sage & Nau 1963; Brenchley 1986). The co-ordinates and local place names for each rookery were extracted from OS maps and recorded by the observers on data sheets. The co-ordinates on the data sheets were entered into the GIS to create a point coverage, and as with the 1996 data, the nest counts were summed into a 5 km cell size grid. For both the 1975/6 and the 1996 coverages, those 5 km cells at the edges of the study area that were not fully surveyed were deleted. For each year, the co-ordinates of each cell with their nest sum value was exported into an ASCII file which was then input into SPSS. To deal with the problem of the suitability of a cell for Rooks to nest in, only those cells with a nest count greater than zero in either of the surveys were considered in further analyses.

Within SPSS the change in nest totals for each of the grid cells was calculated by subtracting each 1975/76 cell value from its respective 1996 cell value.

6.4.2 Environmental data

Data for the mosaic of agricultural land use types covering the study area and the numbers of livestock present were obtained from the Edinburgh University Data Library who provide summaries of the MAFF Parish Agricultural Statistics in a 5 km grid cell format. Due to various new restrictions on the availability of the data, the closest year to 1996 for which data could be obtained was 1988. For comparison with the 1975/6 Rook survey data, 1976 parish agricultural statistics were obtained. The ASCII files contained an easting and northing for each 5 km cell with its hectare values for 14 land use types and totals for three livestock types. The files for the two years were input into SPSS where they were joined to their respective 5 km cell nest count totals via the OS grid reference identifier. Two land use types – woodland and "other land" (which includes land under glasshouses, buildings and ponds) – were unlikely to be used by foraging Rooks and would have incomplete totals for each cell as they also occur outside of farm holdings. Both variables were deleted from the 1976 and 1988 data sets, leaving 12 land use types. Further inspection showed that three cells for 1988 and two for 1976 had no agricultural data and so these cells were deleted from their respective data sets.

Variables representing the changes in the amounts of fields and livestock between 1976 and 1988 were calculated by subtracting the cell values for 1976 from those for 1988.

6.5 Analyses

6.5.1 Data inspection and univariate analyses

Unlike the 1996 nest count data, the accuracy of the 1975/76 data was unknown. No account was given of the area surveyed in 1975/76 and so to check for errors, nest counts for the two years were plotted against one another. Outliers were checked against original field maps and notes, and out of 20 initially identified, three with very low counts were deleted from the 1975/76 sample. For these it was felt that survey coverage had been incomplete in 1975/76, either because this was stated in the original notes (as in one 5 km cell, D. Sowerbutts pers. comm.) or because large rookeries noted in 1996 were not noted in the 1975/76 survey, even though local farmers said they were present at that time. The other 17 cells identified as outliers were retained because rookeries in the same or a similar position were found in 1996 as in 1975/76. Just the counts were very different.

The cell values for the agricultural variables for 1976 were plotted against those for 1988 to check the data for any obvious outliers as most of the variables would not be expected to change by large amounts within an individual cell outwith the patterns evident across its surrounding cells. This procedure identified one outlying cell in the rough grazing plot where the 1976 value was far in excess of that expected considering the 1988 value.

Therefore, this cell was given the average value calculated from its four neighbouring cells in the horizontal and vertical planes.

The final sample sizes used for correlations were: 87 for the 1996 rookery data with the 1988 agricultural data; 80 for the 1975/76 rookery data with the 1976 agricultural data; and 79 for the change between these years. The bivariate scatterplots for the edited data are presented in Figures 6.1 – 6.8.

The 5 km cell nest totals for 1975/76 and 1996 and the habitat and livestock variables for 1976 and 1988 were root or log transformed to normality. Pearson Correlations were used to assess correlations within the agricultural data and the strength of relation of each variable to their respective nest counts. Initial inspection of the correlation matrices for both analyses revealed that amounts of wheat and barley crops were highly correlated ($r > 0.8$) and so these variables were combined to avoid problems of multicolinearity in the multivariate analyses (Tabachnick & Fidell 1996). This combined tilled land variable also included five crops (fallow, oats, potatoes, rape and vegetables) which were underrepresented (< 20 hectares) in most of the 5 km cells. A summary of the field and livestock types used is given in Table 6.1.

Spearman Rank Correlation coefficients between changes in the amount of crops and livestock from 1976 to 1988 and nest counts from 1975/76 to 1996 were also calculated.

Table 6.1 Summary description of the field types and livestock categories.

Variable	Description (adapted from survey questionnaires, A. Bayley pers. comm.)
Grass < 5yr	Grass leys of *Lolium perenne* and *Trifolium* spp. less than 5 years old, cut for hay and silage and/or grazed by livestock
Rough grass	Heath, moor, down or other rough land used for grazing whether enclosed by fencing or not
Grass > 5yr	Improved pastures that do not include land in the above two categories, probably grazed by livestock and sometimes used for cutting
Tilled land	*Triticum aestivum*, *Hordeum vulgare* (spring and winter types), *Avena sativa*, *Brassica napus* crops plus scattered fields of *Solanum tuberosum*, *Brassica* sp., *Lathyrus* sp. and land left fallow
Total cows	Includes all males, females and young
Total pigs	Includes all males, females and young
Total sheep	Includes all males, females and young

6.5.2 Multivariate analyses

Those variables with significant Pearson Correlation coefficients from the within-year comparisons were entered into forward stepwise multiple regressions. Those variables with significant Spearman Rank Correlation coefficients in the between-year comparison were checked for normality before entry into a simple linear regression. The three resulting equations were used to predict nest counts for both survey periods and the change in nest counts between them. Spatial plots of the residual cell values were used to detect any other geographic trends in the data (Goodchild 1986).

6.6 Results

6.6.1 Changes in the variables between years

The number of nests per 5 km cell shows a general increase from 1975/76 to 1996 in the study area (Fig. 6.1). Some cells have maintained roughly the same number of Rook nests over this period, whilst others have shown large increases or decreases. As the outliers in the 1975/76 data set have been removed, it is thought that these represent real changes.

The gradual shifts apparent in the field and livestock data between years give confidence in the data for the individual years. If large changes in individual cells had been apparent, with no consistent pattern, this would have cast doubt on the reliability of the agricultural data and their usefulness to further analyses.

Compared to the reference lines given in Figures 6.2 – 6.8, three patterns can be seen in the agricultural changes that occurred between 1976 and 1988: the number of hectares of grass less than five years old (Fig. 6.2) and the total number of cows (Fig. 6.6) have generally decreased; the area of tilled land (Fig. 6.5) and the number of sheep (Fig. 6.7) have generally increased; and the areas of grassland more than 5 years old (Fig. 6.3) and of rough pasture (Fig. 6.4) have remained remarkably constant. The total number of pigs (Fig. 6.8) shows no particular pattern of change.

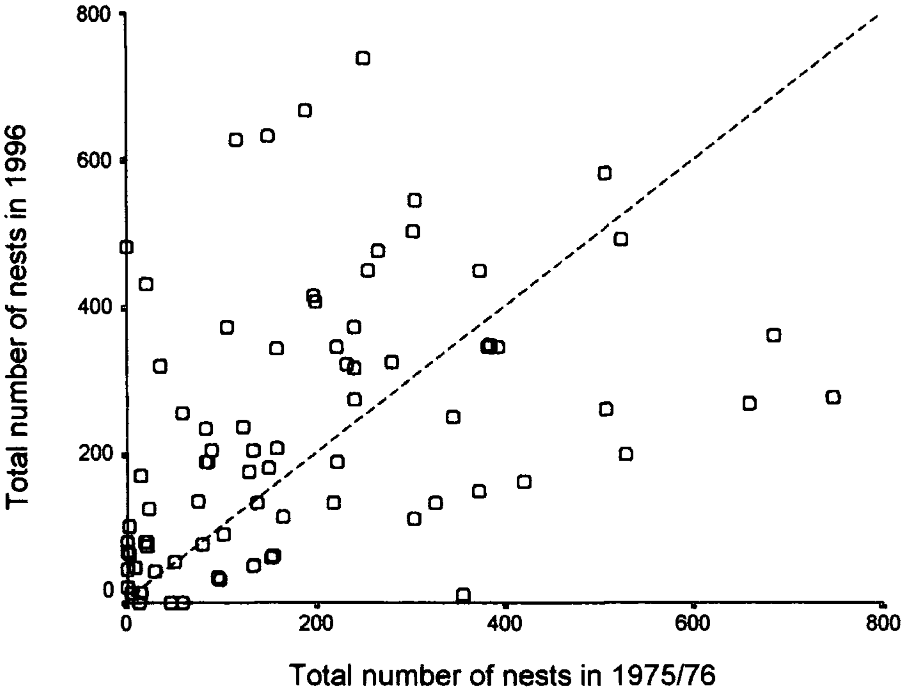


Figure 6.1 The total number of nests per 5 km cell in 1996 compared to 1975/76. (-----) = equality between years

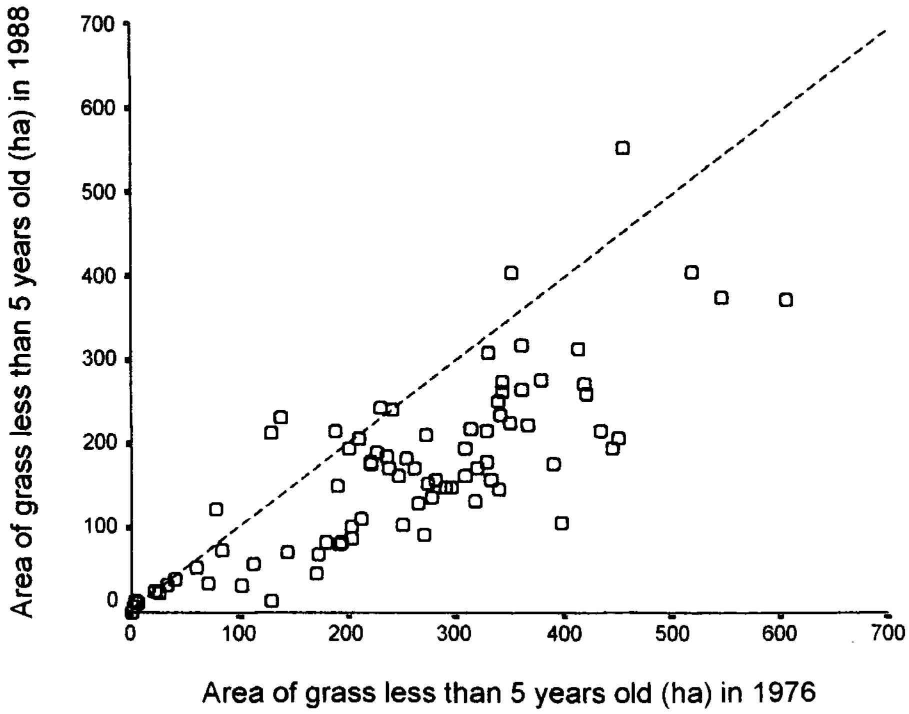


Figure 6.2 The total area of grass less than 5 years old per 5 km cell in 1988 compared to 1976. (-----) = equality between years

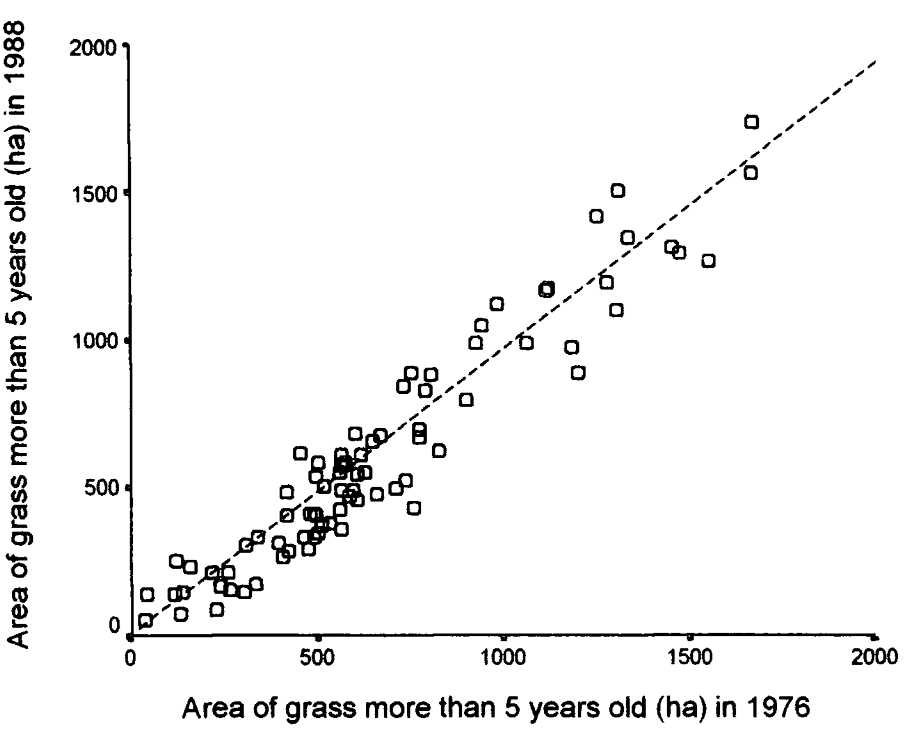


Figure 6.3 The total area of grass more than 5 years old per 5 km cell in 1988 compared to 1976. (-----) = equality between years

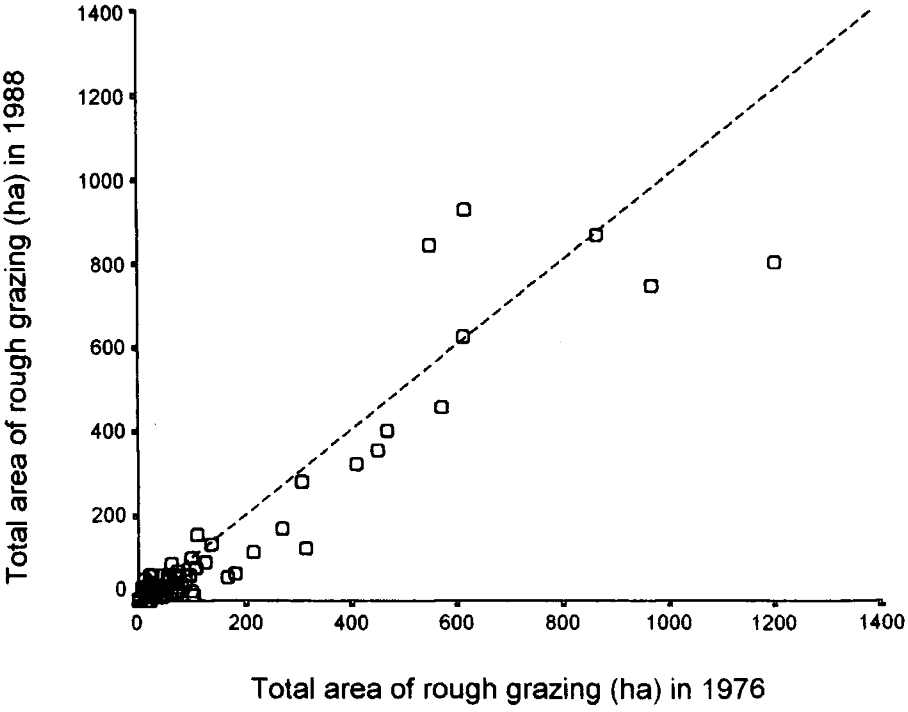


Figure 6.4 The total area of rough grazing per 5 km cell in 1988 compared to 1976. (-----) = equality between years

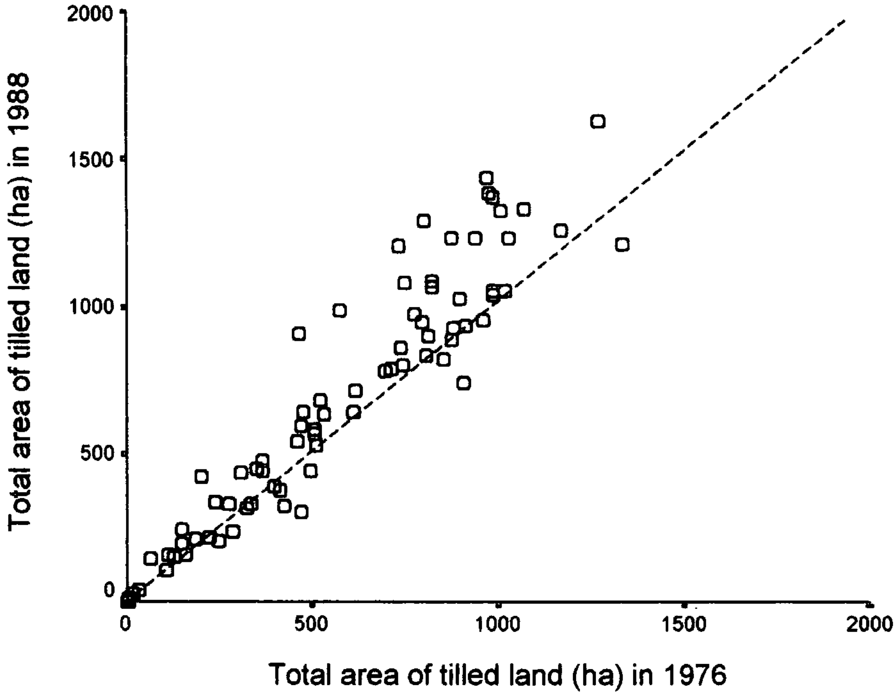


Figure 6.5 The total area of tilled land per 5 km cell in 1988 compared to 1976. (-----) = equality between years

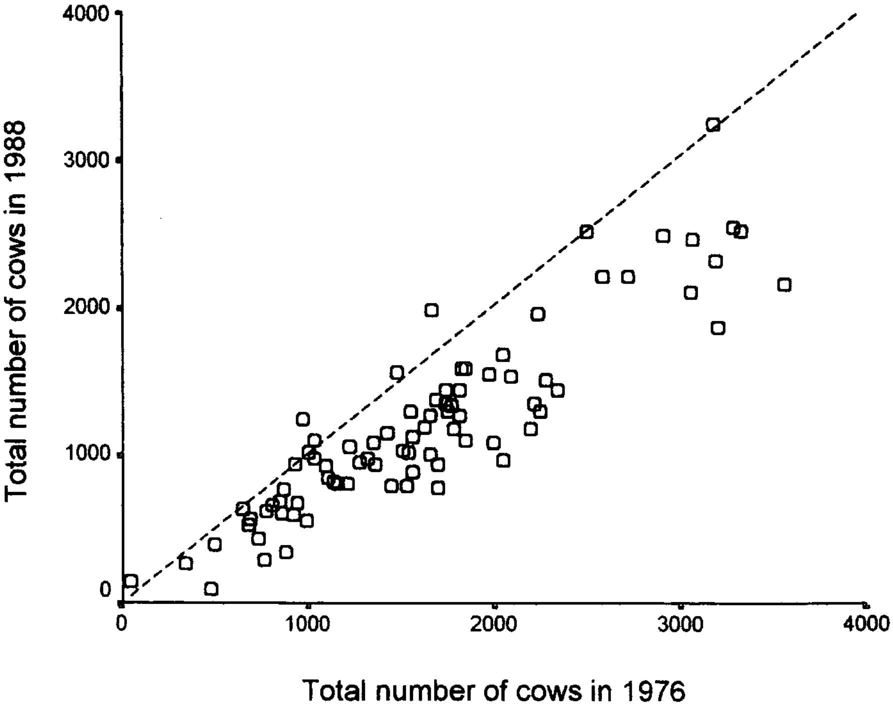


Figure 6.6 The total number of cows per 5 km cell in 1988 compared to 1976. (-----) = equality between years

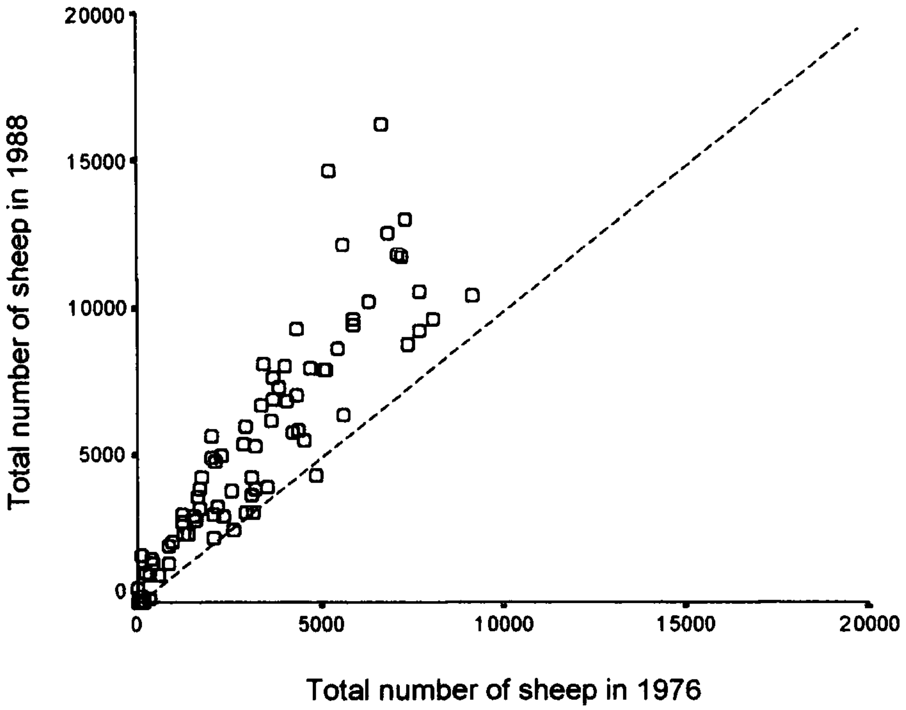


Figure 6.7 The total number of sheep per 5 km cell in 1988 compared to 1976. (-----) = equality between years

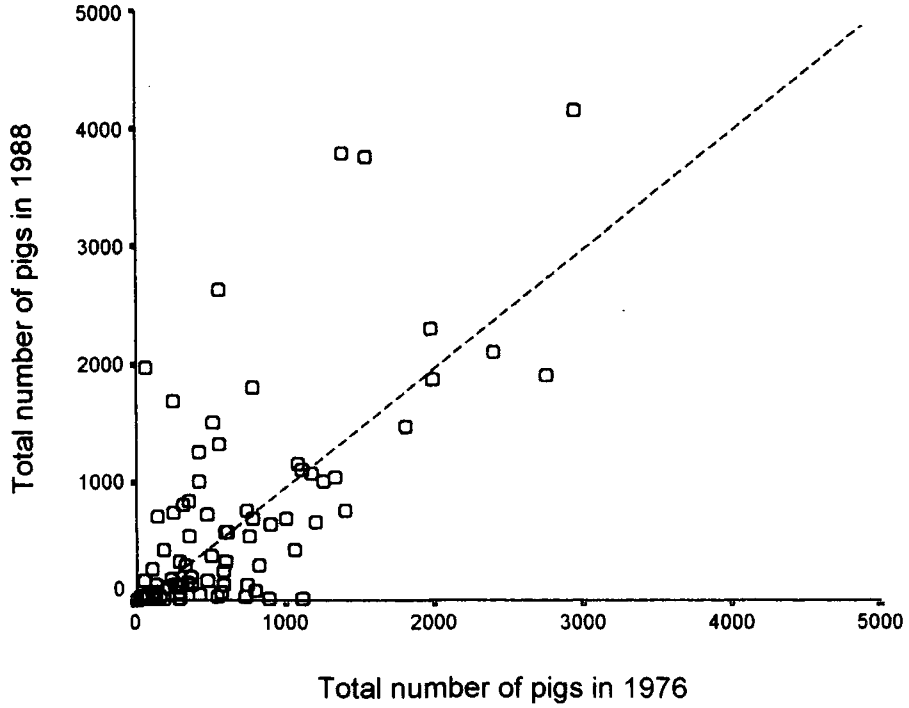


Figure 6.8 The total number of pigs per 5 km cell in 1988 compared to 1976. (-----) = equality between years

6.6.2 Univariate correlations

The correlations of the 1976 agricultural data with the nest data for 1975/76, and the correlations of the 1988 agricultural data with the nest data for 1996 are shown in Table 6.2. It can be seen that only the amount of tilled land and grasslands less than 5 years old have significant correlations with the number of nests per 5 km cell in 1975/76. In 1996 all variables are significantly correlated with nest counts, although grasslands less than 5 years old again show the strongest positive correlation. Only the amount of rough grass is negatively correlated with the number of nests. As expected the total cow and sheep variables have a close association with grasslands. Although this means that to a certain extent, the livestock variables represent the pasture types, they will still be used in the stepwise multiple regression as these parameters may combine to model Rook numbers in relation to the intensity of pasture use.

Only the change in the total number of sheep in a 5 km cell was significantly correlated with the change in the number of nests between survey periods ($r_s = 0.36$; $P < 0.01$).

Table 6.2 Pearson Correlations between all agricultural variables and the nest count totals for the 5 km cells for 1975/76 and 1996.

	Pearson Correlation Coefficients for 1976 (*n* = 80) and **1988 (*n* = 87)**							
Transformation	root	-	log	root	-	root	root	root
Variables	Nests	Grass < 5yr	Rough grass	Grass > 5yr	Tilled land	Total cows	Total pigs	Total sheep
Nests	1.000/**1.000**							
Grass < 5yr	0.366**/**0.525****	1.000/**1.000**						
Rough grass	-0.144/**-0.379****	-0.214/**-0.165**	1.000/**1.000**					
Grass > 5yr	0.043/**0.322****	0.180/**0.298****	0.365**/**0.212***	1.000/**1.000**				
Tilled land	0.363**/**0.260***	0.665**/**0.467****	-0.217/**-0.324****	-0.246*/**-0.326****	1.000/**1.000**			
Total cows	0.220/**0.496****	0.638**/**0.722****	0.190/**0.063**	0.718**/**0.711****	0.226*/**0.154**	1.000/**1.000**		
Total pigs	0.184/**0.272***	0.403**/**0.373****	-0.201/**-0.206**	-0.023/**0.155**	0.483**/**0.339****	0.326**/**0.401****	1.000/**1.000**	
Total sheep	0.006/**0.239***	0.083/**0.314****	0.512**/**0.385****	0.728**/**0.806****	-0.341**/**-0.293****	0.530**/**0.665****	-0.294**/**0.130**	1.000/**1.000**

* $P < 0.05$ ** $P < 0.01$

6.6.3 Multivariate models

Of the two independent variables entered into the stepwise multiple regression with the 1975/76 nest data, only grassland less than 5 years old was retained by the model. The variance explained was 12%. For the 1996 nest data the variance explained was higher with 41% accounted for by the three grassland variables. The variables and their parameter estimates, in the order of their entry into the equation, are given below:

$$Y = 0.02373x_a - 3.595x_b + 0.236x_c + 10.473$$

Where x_a = the area of grass less than 5 years old, x_b = the $\log_{10}$ transform of the area of rough grass, and x_c = the root transform of the area of grass more than 5 years old. Again grassland less than 5 years old was the most important predictor of the 5 km cell nest totals.

Changes in the cell nest counts between the 1975/76 and 1996 survey periods were related significantly to changes only in the total number of sheep across the area. This variable explained 20% of the variation in nest count changes in the 5 km cells.

Spatial plots of the residuals from all three regression models showed no geographical patterns, thus only those from the best model (1996 data) are presented (Fig. 6.9).

The total nest number across the study area was 14870 for 1975/76 and 18470 for 1996, representing a 24% increase. This increase does not appear to have been uniform with the highest positive changes occurring in the western parts of the study area and the highest negative changes occurring in the eastern and central parts (Fig. 6.10).

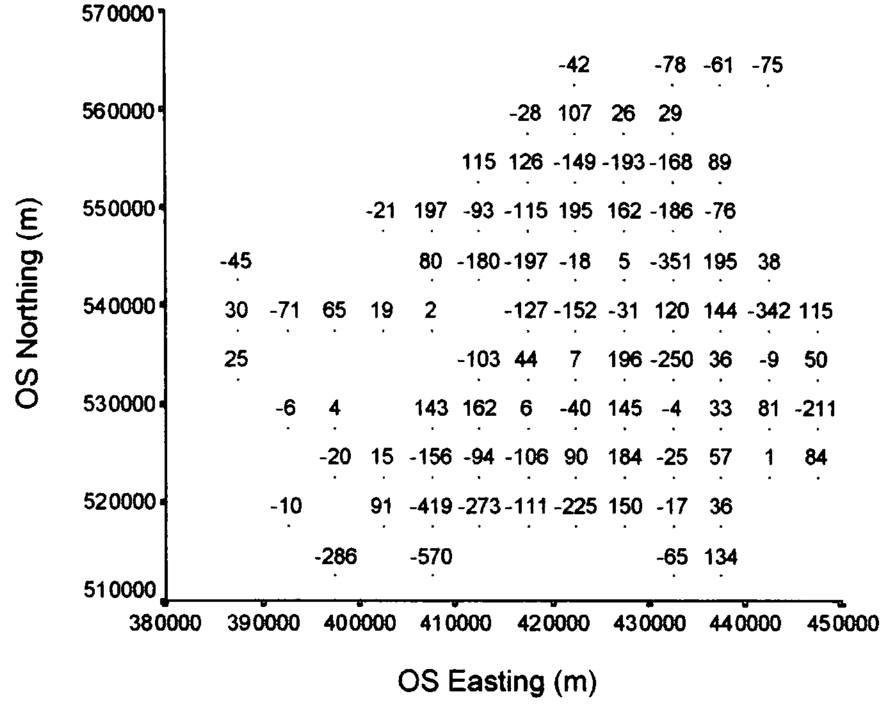


Figure 6.9 Nest count residuals per 5 km cell for the regression model using 1996 Rook survey data with 1988 agricultural statistics.

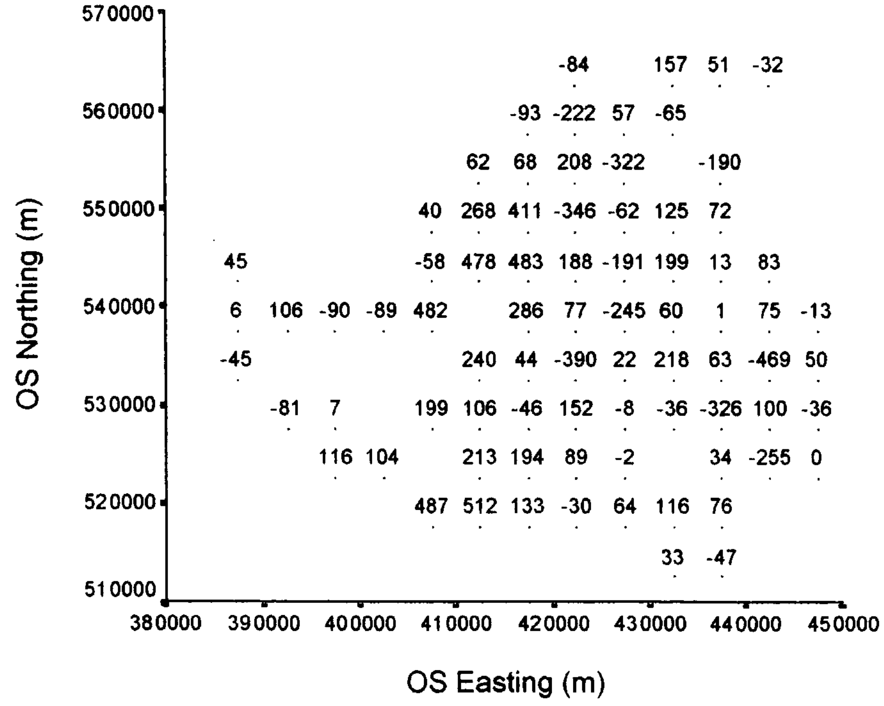


Figure 6.10 Nest count changes per 5 km cell from 1975/76 to 1996.

6.7 Discussion

Both the 1996 and the 1976 models of the spatial variation in Rook numbers across the study area offer support for the findings of Chapter 5. The models show that Rook numbers within 5 km cells are most highly related to those grasslands less than five years old. These newly seeded pastures probably represent those cut for silage and hay production. This partly explains the positive correlation with livestock numbers (Table 6.2), although some of these pastures will also be used for grazing. These newly sown pastures whether cut and/or used for grazing are likely to be classified as Mown/Grazed Turf by the ITE data (Chapter 3), the variable explaining most of the variation in individual colony size (Chapter 5).

The model for 1996 is likely to be more robust than that for 1975/76 as survey coverage of the study area was more exhaustive. Also the accuracy of the nest counts for 1975/76 would have been reduced because of the variation between observers in deciding what constitutes a nest in nest clumps and the willingness to gain access to colonies rather than counting them from a distance (Brenchley 1986). This was evident in 1997 when my nest counts at colonies were compared to those recorded during a partial BTO survey in 1997.

The very low totals for some of the cells in 1996 compared to 1975/76 (Fig. 6.1) do not represent errors in the 1996 data, and were possibly due to intensive shooting of the rookeries in these cells which can cause reductions in Rook numbers in areas of lower breeding density (Wright 1966). However, Dunnet & Patterson (1968) suggest that variations in nest numbers between years are not related to the numbers of young shot.

Initial differences between the proportions of young in flocks in June around unshot and shot rookeries are quickly eliminated, probably by the rapid dispersal of juveniles once they leave their natal rookeries (Dunnet *et al.* 1969). The extent to which rookeries were shot across the whole study area remains unquantified and is likely to be an unmeasured variable affecting model performance. Nevertheless, both models did identify the same primary habitat correlate with Rook numbers. The 1996 model also showed Rook numbers were positively related to older pastures. These are more likely to be the permanent pastures used for sheep and cattle grazing which also form a major component of the Mown/Grazed Turf ITE category, and possibly some of the less intensively managed fields in the Meadow/Verge/Semi-natural ITE category. The negative correlation with rough grazing suggests that these taller grass communities, predominantly in the upland areas of the west, are of little use to Rooks. The positive correlation with cut and grazed pastures was not unexpected considering the number of studies that have observed the importance of these field types to foraging Rooks (Feare *et al.* 1974; Feare 1978; Waite 1984; MacDonald & Whelan 1986; Barnes 1997) and to other invertebrate eating birds in general (Wilson *et al.* 1996). Brenchley (1984) found a similar relationship of increasing Rook density with increasing proportion of grassland over much of Scotland. In England and Wales however, Rook density increased as the proportion of grass increased to 55% of the area of agricultural land, but decreased above this value. Similarly, Rook density increased up to a tillage area of 41% but decreased thereafter. Thus high Rook densities were associated with optimum levels of these two major agricultural land use types.

As stated in Chapter 5, the lack of finer habitat divisions coupled with the lack of spatial explicitness in the habitat cell totals for the agricultural statistics has probably led to weaknesses in the models. The models could also have been improved if Rooks within one cell had been allowed to contribute to the totals for neighbouring cells by smoothing of the data. This would have avoided the arbitrary assignment of rookeries at the edge of a cell to that cell when rookery members are very likely to use habitat attributed to other cells. Such a smoothing process though, which is similar to that used in Chapter 5, is computer intensive and causes problems where Rooks are assigned to cells without, or with very little, suitable habitat. Smoothing changes the number of cells which can be used for model building and creates problems when comparing the variance explained by one model with another. Preliminary analysis using smoothed data suggested that although the variance explained showed no strong pattern of increase or decrease with the distance over which Rook numbers were smoothed, the same variables remained important in all models. Thus, the use of this independent source of habitat data from MAFF supports the gross predictions of the colony specific model produced from the ITE data (Chapter 5), and the suggestion that a finer division of pasture types is important. Also, the models produced in this chapter may be of more general use for testing spatial and temporal patterns in data collected in other Rook surveys as they are less complex and computer intensive to produce.

When analysing changes through time in the Rook population, the inaccuracies of the 1975/76 survey data coupled with slight shifts in the rookery distribution will obviously have knock-on effects for the calculation of nest number changes from then until 1996. The inference that the change in nest totals is not just a between year anomaly can only be accepted when the magnitude of change (Fig. 6.1) is compared to that seen between consecutive survey years (Chapter 2).

Only the total number of sheep per 5 km cell showed any significant relation to changes in the number of Rooks per 5 km cell. The highest increases in Rook numbers were recorded in the west of the county where the farming is predominantly pastoral, and the highest decreases were recorded in the east and central areas where arable farming has greater importance (Fig. 6.10). This partly agrees with the findings of Lomas (1968) who showed that the decline in Rook numbers in Derbyshire was greatest where the concentration of grain growing was highest. However, the study only cited a crude visual comparison between a map of the changes in Rook numbers from 1944 and 1966 overlaid onto a map showing the percentage of tilled land in 1966. From this, Lomas (1968) inferred a negative correlation between changes in Rook numbers and changes in the amount of tilled land. Such a correlation was not found in the current study, where the true change in land use was calculated.

Another interpretation of the relationship found by Lomas (1968) would be that where the percentage of pasture (the other main constituent of the land use percentage) was greatest, Rook numbers would have increased or remained the same. This temporal correlation of pasture with nest numbers was also not found in the current study. Thus, although a similar pattern of Rook number decrease in arable areas and increase in pastoral areas was found in the current study, the study of Lomas (1968) and in national surveys (Sage & Whittington 1985), it does not appear to be due to changes in the percentage of arable and pastoral field types. This was unexpected, considering the findings of the models for the spatial distribution of Rooks within years. Instead, changes in the number of sheep (Fig. 6.7) appear to be important, possibly because this has counteracted the increase in the amount of tilled land (Fig. 6.5) that has occurred at the expense of pasture (Fig. 6.2 + 6.3), by increasing the forage quality of those pastures remaining. In Brown-headed Cowbirds (*Molothrus ater*), subtle differences among pastures can affect feeding group sizes, with grass height being of secondary importance to the presence of grazers probably because they increased the availability of invertebrates within the pastures (Morris & Thompson III 1998). Therefore in the present study, the increased number of sheep may have increased the availability of insect food as well as other stock feed to Rooks leading to an increase in their numbers. The total number of sheep per 5 km cell may not have been identified as the most important factor in the spatial models within years because it is not the number of sheep *per se* that is important but rather this hypothesised interaction with pastures. Figure 6.7 shows that the sheep numbers have almost doubled in most of the 5 km cells from 1976 to 1988 whilst the area of pastures on which they are kept has stayed roughly the same. Therefore stocking rates appear to be important as found for changes in Rook numbers from 1978 to 1988 for an area in western Wales (Chater 1996).

The pastures used for grazing in the study area were mainly older improved grasslands, although some rough grasslands and meadow were utilised in marginal areas (pers. obs.). Newly sown leys were less extensive in 1988 than 1976 (Fig. 6.2), possibly accounting for the increase in the proportion of tilled land over this period (Fig. 6.5). Newly sown leys are only important to foraging Rooks for up to about 5 days after they are cut for silage production (pers. obs.; Barnes 1997). Older re-seeds become richer in invertebrates through time, whilst the grazing of rough grass and meadows can render subterranean invertebrates more readily available to Rooks (C.J. Feare pers. comm.).

To conclude therefore, it seems that spatial variation in Rook numbers in County Durham is correlated with the density of pastures whereas temporal variation in Rook numbers is correlated with changes in sheep numbers across the study area. The reason for this difference in the factors identified is not clear, although it is possible that changes in the amounts of pasture have been obscured by changes in sheep stocking regimes. On the other hand, the variation in total sheep numbers across the study area was positively correlated with Rook numbers in 1996, as were cattle numbers (Table 6.2), suggesting the importance of grazers. However, these variables did not enter the model produced, as the pasture variables explained slightly more of the variance. The method used for collecting the agricultural returns may account for the difference in the predictive power of these variables, as sheep and cattle are attributed to a farm holding in a parish even when grazed in areas away from that parish. Perhaps only the changes through time were of sufficient magnitude to identify this variable.

Even so, it seems likely that there is some interplay of grazers with pasture and that this is correlated with the food resource important to Rooks. Active sheep pastures were indeed observed to be important to foraging Rooks in County Durham (Barnes 1997).

A final possibility is that as sheep numbers are correlated with an east/west cline in altitude across the area, the increase in Rooks to the west and the decrease in the east may correspond to climatic changes, such as an amelioration of winter temperatures or different rainfall patterns, which have affected food availability within the pastures. This could account for the difference between the factors identified in the spatial and temporal models.

The findings of this chapter, coupled with those of Chapter 5, suggest that a model of individual colony size would benefit from an accurate habitat map of localised variation in pasture type. Gathering this detail over large areas is probably only possible "on foot" or through the use of aerial photography. If grazing and cutting are important features then this information would need to be gathered many times during the year to identify the temporal pattern of resources and the period during which they limit Rook numbers. Other factors such as water content through time and soil type may need to be considered as these also have subtle effects on the foraging quality of pastures. It would be worth concentrating on the pasture resource as tilled land appears to have little importance, as found in Wales (Chater 1996).

6.8 Summary

Regression models based on 5 km cell totals of Rook numbers for 1975/76 and 1996 in relation to MAFF habitat data for 1976 and 1988 respectively, supported the finding that Rook numbers are broadly correlated with pasture and not with the amount of tilled land. The models differentiated between pasture types, with the amounts of grassland less than 5 years old being important to both models. The variance explained in the 1975/76 Rook data was 12% whilst for the 1996 data it was 41%.

Changes in Rook numbers from 1975/76 to 1996 were correlated (20% of variance explained) with changes in sheep numbers, rather than land use. The reasons for this difference between the variables identified in the within- and between-year models are discussed. The findings suggest a potential interaction between grazers and pastures in the form of stocking rates, and further investigation of the importance of specific pasture types to individual colonies in terms of their spatial position and temporal use is advised.

Chapter 7

7 Final discussion, conclusions and future work

The causes of variation in colony size and the evolution of coloniality in birds are poorly understood (Brown *et al.* 1990; Danchin & Wagner 1997). There have been calls to examine the direct effects of food availability on colony size in more species as these often remain largely unmeasured (Brown 1988; Cairns 1992). The distribution of food resources is a precursor for many theories relating to colony size variation and the evolution of coloniality through individual selection. However, although it is presumed that food supplies provide an upper limit to colony size (Ashmole 1963; Lack 1968) the extent to which it contributes to variation in colony size is often unknown.

Food supplies may act directly on colony size, or indirectly through competition where the same foraging area supports the members of more than one colony. Studies have shown the separate effects of competition (Furness & Birkhead 1984; Hunt *et al.* 1986; Ainley *et al.* 1995) and food supplies (Gibbs *et al.* 1987; Møller 1987; Bustamante 1997) on colony size, but none have investigated the distance over which their potential interaction is strongest. Studies have either made assumptions about the distribution and availability of food (Ainley *et al.* 1995; Furness & Birkhead 1984; Wiklund & Andersson 1994) due to the difficulties of measuring it directly (Diamond 1978; Cairns 1992), or where food availability can be measured, have made assumptions about the area over which it is important to colony size (Gibbs *et al.* 1987; Møller 1987; Bustamante 1997). This leads to deficiencies in the models produced which causes difficulty when trying to assess the importance of additive effects or the extent to which the underlying assumptions do not hold.

Therefore, the principal aim of this thesis was to quantify the extent to which Rook colony size relates to the interaction of competitors with the foraging resource, and the distance over which this occurs.

To tackle this question, it was necessary to establish a data base of the extant variation in colony size of the Rook across the study area. With a single observer covering such a large area, counts had to be made over a series of weeks, and so the effect of count date had to be minimised. Therefore, the period over which nest changes were minimal was established. In 1995, this period was judged qualitatively, as colonies in the area were still being discovered. In 1996, nest changes were followed more closely for a sample of colonies, and this showed that there was no significant change in nest numbers after 9 April until the end of that month. This agreed with the qualitative impressions gained in 1995 and 1997. Thus, comparable nest count data were obtained for three years and this demonstrated that the spatial differences in nest counts across the area were consistent and were not an artefact of the survey technique or stochastic variation between years. Chapter 2 therefore established the phenomenon under study, and the techniques developed in that chapter could probably be applied to similar study species.

Field observations suggested that colony sizes would show some broad relation to the habitat type in an area. However, it was noted in many places that colony spacing was not regular and that, before further analysis, some attempt at defining colony units would have to be made. It was felt that colony spacing exhibited at least two patterns, and that those leading to the separation distances observed in colony clusters were below the spatial, and probably temporal, resolution of the datasets used in this thesis. Therefore, the distance over which colonies were clustered was determined using a simple technique within the GIS, which suggested colony units up to 500 m from one another should be combined. This decision, although based purely upon the spatial relationships within the data, was backed up by personal observations of overlap in foraging areas within the study area and by the findings of an MSc project (Barnes 1997) undertaken in 1997 during the term of this thesis. This division of colony units also corresponds to the distance over which behavioural interactions take place, such as the "nuptial flights" (Coombs 1961a) above colonies. For a limited number of rookeries in Scotland, Patterson *et al.* (1971) also recorded high levels of behavioural interaction and foraging range overlap between units about 500 m apart, with little occurring beyond 1 km.

Having established a meaningful colony unit, preliminary analysis of how Rook colony sizes relate to one another and to the habitat was undertaken. This immediately revealed a problem, and in contrast to what might be expected there appeared to be little direct correlation of Rook numbers with habitat variables. It was thought that this problem could be due either to competitive interactions, or to inaccuracies in the ITE habitat map. Therefore in Chapter 3 I examined, as thoroughly as possible, the potential sources of inaccuracy within the ITE habitat data. Disappointingly, it became clear that even when taking the likely rates of historical change into account (based on inspection of aerial photos taken around the date of satellite image acquisition), there was confusion between the habitat types within which Rooks show foraging preferences. The main finding was that, contrary to the ITE description, frequently cut pastures tended to be identified as Mown/Grazed Turf rather than Meadow/Verge/Semi-natural. Although the findings cannot necessarily be extended to other geographical areas outside County Durham, it suggests that other studies utilising this data should be cautious, especially where the habitat is likely to be as dynamic and dissected as the agricultural mosaic studied here. These findings also confirmed that the data would be of little use in analysing very localised differences in Rook distribution, but would perhaps be useful for identifying broader trends in relation to the relative amounts of habitat across larger areas. Even so, the main aim of this thesis was compromised by the lack of accuracy in the ITE data, as it would not allow quantification of the degree to which results did not fit the Ideal Free Distribution due to other social aggregative factors (Brown & Rannala 1995).

Foraging habitat is not the only feature to be considered by a Rook assessing an area in which to breed. An area will also need to contain a suitable woodland nesting habitat. In Chapter 3, it was shown that the ITE woodland classes identified only 43% of the woodlands used for breeding, and also depicted non-woodland areas as woodland. The performance of the ITE data was related to woodland size, and the findings of Chapter 3 closely matched those of Mack *et al.* (1997) for East Anglia, giving confidence in the methods used to assess the accuracy of the ITE data overall.

Therefore, the ITE data were thought to be of little use in assessing the geometric and species composition characteristics of woodlands, and therefore the extent to which this resource affected the distribution of colonies.

Due to the many shortcomings of the ITE data, the potential of using the digital OS data directly to model Rook nesting habitat was investigated in Chapter 4. OS data have been used in this way previously (Austin *et al.* 1996), and it was argued in Chapter 4 that the coarse-level identification of breeding habitat would, within reason, represent the finer-level availability of nest sites. The OS woodland data correctly identified 65% of the rookery woodlands and classified 95% of them to the correct woodland type. Therefore, as the OS woodland data performed better than the ITE woodland data, they were used in a logistic regression to compare the attributes of a random set of woodlands to the set occupied by Rooks. There was considerable overlap between the two sets in terms of the landscape variables measured to define them. This suggests that there are many suitable woodlands within the landscape that are unoccupied, and thus a shortage of nesting habitat is highly unlikely to have caused the aggregations of nesting Rooks recorded. This supports the findings of Murtland (1971) for Rooks in the Ythan catchment in Scotland and so it seems this factor is unlikely to be important in an evolutionary context for this species, in most situations.

In Chapter 5 I tested whether the set of sites identified as suitable were likely to be so when the exploitation of food resources over larger distances by the members of neighbouring colonies was taken into account. Originally it was thought worthwhile only to test colony sizes against amounts of habitat within typical foraging ranges observed during the breeding season (as in Gibbs *et al.* 1987; Møller 1987; Bustamante 1997). However, even with the 500 m definition of a colony unit, it became clear that overlap in the theoretical foraging ranges constructed within the GIS was considerable. This suggested that the foraging habitat in many areas could be providing food for the members of more than one colony. Therefore the modelling approach adopted by workers investigating the range over which competitive interactions between the members of neighbouring colonies are strongest (Furness & Birkhead 1984; Hunt *et al.* 1986; Ainley *et al.* 1995), was applied to the investigation of the interaction of competitors and foraging habitat on colony size. However, the approach was modified because these studies treated all colony members of all colonies over a foraging range as potential competitors. This was thought unrealistic and so a method was devised that used cubic equations to calculate the expected number of competitors around each colony based on their distance from neighbouring colonies, with the number of competitors being proportional to the overlap between colony foraging ranges. Also, colony counts were reassigned to colony locations at random, to test for the generation of any spurious relationships between Rook numbers and the amounts of each land use type, as the distance over which interactions were tested was increased.

The multivariate model produced explained 31% of the variance, and showed how the availability of habitat and interactions with competitors up to 6 km could be important determinants of colony size. This was an important finding as it suggested that Rook colony sizes may be limited by factors acting outside of the breeding season (as suggested for seabird species, Lack 1966; Diamond 1978; Ainley *et al.* 1995). This contrasted with the findings of Chapter 4 where habitat within about 1 km of a woodland influenced whether or not it was colonised by Rooks. This may be because the habitat close to the colony is important during the breeding season – when Rooks forage about 1 km from their colonies (Barnes 1997) - and thus to initial site selection, whereas the habitat and competitive interactions outside the breeding season influence the eventual colony size. Even with the problems in the ITE data, the iterative modelling identified the Mown/Grazed Turf as being of prime importance in determining the position and size of the rookeries. This finding is in accord with observations of foraging Rooks in the field (Feare *et al.* 1974; Feare 1978; Purchas 1980; Waite 1981; MacDonald & Whelan 1986; Barnes 1997).

Through the use of an independent source of habitat data provided by MAFF, the proposed relation between Rook numbers and pasture in Chapter 5 were verified. However, the MAFF data allowed for a finer breakdown of pasture types and gave an indication that there is indeed a differential influence of pasture quality on the spatial distribution of Rook numbers. Chapter 6 demonstrated that taking subtle management and stocking regime effects into account may allow for the construction of a better model with greater predictive power. It is suggested that Synthetic Aperture Radar (SAR) remotely sensed data may be more appropriate for the detection of subtle differences in habitat type, and for following temporal changes in habitat, as they are available more often than Thematic Mapper (TM) scenes.

Overall, Chapters 5 and 6 show a spatial relationship of Rook numbers to spatial variation in the availability of the probable foraging resource, and a temporal response to changes in its quality. Both of these findings are consistent with the IDF theory of the distribution of individuals among colony sites in relation to food supply. That there is not a precise match i.e. that there is a large component of unexplained variance in all the models, is possibly due to the imprecise environmental data (Chapters 3 & 6) coupled with the assumptions made on foraging range use and shape (Chapter 5). However, Chapter 5 does suggest that larger colonies are larger than expected which may be due to some sort of social attraction effect (Danchin & Wagner 1997) acting in conjunction with the IDF distribution (Brown & Rannala 1995). The findings of Chapters 4 and 5 suggest there might be gaps in the distribution of Rook colonies. Again, although any conclusion is weakened by the quality of the ITE data, this supports the idea of social attraction. Applying Sibly's (1983) model of optimal group size choice to coloniality, individuals will continue to aggregate at a colony whilst fitness pay-offs at that site are perceived to be better than those for other colonies sampled in an area, or for the individual nesting alone. The individuals joining may depress the fitness levels of those already present below optimal levels (Sibly 1983; Danchin & Wagner 1997). This suggests that members of a colony might seek to repel prospecting birds above a certain colony size, or should advertise their success in relation to other colonies and thus aid information gathering and individual choice.

In the models produced, deviations from the expectations of IDF theory were not thought to be due to different quality individuals nesting in different colony sites or sizes. The sample of colonies observed in Chapter 2 followed the same general pattern of nest build-up and did not exhibit the sequential colonisation of the nesting habitat seen in the Sand Martin, where sub-colonies containing individuals of a similar age are produced (Jones 1987). However, age or quality effects cannot be discounted, and may explain the possible reduced synchrony of completion of nest-building in smaller colonies (Chapter 2), as suggested by Brown *et al.* (1990). This however, is more likely to be accounted for by reduced social stimulation (Møller 1981).

In foraging theory, lags in information obtained about the foraging habitat are hypothesised to cause deviation from an IDF distribution (Milinski & Parker 1991). This lag effect could be an important cause of unexplained variance in the Rook models. Chapter 4 shows how some colonies may be located purely within arable crops which are little used for foraging. The members of these colonies were often observed foraging at refuse sites, although the colony position possibly originally related to pasture which has since been converted, as woodlands were often planted to provide cover for livestock. The reason for Rooks remaining at a site that would not now be colonised is probably more related to social attraction than to information effects in the Rook, as habitat patches are fairly consistent between years and so there would seem to be ample time for assessment in a bird which is resident at or near the colony throughout the year.

The nature of individual habitat choice is central to the theory of the formation and evolution of colonies, as has been emphasised by Danchin and Wagner (1997). Their "bottom-up" approach has intuitive appeal because the individual's choice becomes the unit for selection and evolution. Through their model the colony is seen as resulting more from a behavioural response to the landscape and conspecifics, and much less as a fixed evolutionary structure. This is not to suggest that the other hypotheses introduced in Chapter 1 have no relevance. Rather, their importance may differ across species and habitats so that they are best combined and assessed in terms of a single variable such as reproductive success. Siegal-Causey and Kharitonov (1990) noted that many studies have proposed various selection scenarios leading to coloniality in terms of the trade-offs between the advantages and disadvantages of group nesting. They consider that this approach suffers from possible confusion between the consequences of coloniality and the critical factors leading to its evolution. In Danchin and Wagner's (1997) model, advantages and disadvantages are distilled into a single measure, and coloniality arises from individual assessment of a proximate indicator of group success.

Therefore, considering the potential importance of individual choice to the functioning of colonial systems, future research should perhaps concentrate on the cues which prospecting individuals are exposed to, perceive and act upon.

The distribution and abundance of food resources is the “template” on which many theories of coloniality are based. This is more amenable to study in the Rook than in many other bird species. The current study shows how two fairly simplistic data sets (bird and habitat data) can be integrated within a GIS to gain an understanding of possible foraging interactions occurring over large distances and how closely the distribution of individuals among colonies conforms to current theory. This use of GIS for elucidating behaviour is an expansion of its more traditional use for predicting whether or not a habitat will be occupied by a species.

The predictions arising from the spatial modelling approach adopted in this thesis could be tested and extended using field based procedures.

- Using marked individuals, the hypothesis that there is movement of breeding birds between years among colony sites, especially over distances of about 500 m within the clusters identified, could be tested.
- Coupled with genetic studies, marking could identify whether the groups of individuals that appear to shift location are a more closely related cohort than expected, and thus whether the colony unit has a genetic definition smaller than the purely spatial definition of nest groupings.

- Genetic studies could also be used to identify whether extra-pair matings occur, as is prevalent among other colonial species. Coupled with studies of reproductive success this may help to clarify why certain individuals, groups or whole colony units shift location.
- Data on reproductive success could be linked with refined models of woodland suitability for nesting, based on habitat maps with an improved classification of grassland types, derived from satellite data collected at a greater temporal resolution. By grading woodlands according to suitability, the extent to which locational shifts represent habitat based decisions and/or those based on reproductive success could be assessed. Low rates of natural movement could perhaps be enhanced by forced evictions.
- The distances over which individuals utilise the habitat, or sample colony site characteristics could be quantified using telemetry, and/or marked individuals. This would also give an idea of the frequency of occurrence of such behaviours.

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Appendix

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Colonization patterns at Rook *Corvus frugilegus* colonies: implications for survey strategies

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The increase in Rook Corvus frugilegus *L. nest numbers at 18 colonies in County Durham, UK was monitored during the spring period of colony build-up. Nests were mapped to avoid miscounts and to track the stages of nest completion. Colonies were asynchronous in reaching maximum numbers, although all followed the same general pattern. Despite large variation in initial colony size on 1 April, a constant proportional increase up to the modal date of maximum counts on 21 April was recorded. The implications for survey strategy are discussed.*

Surveys are an important means of identifying the population trends of a species. For robust comparison of numbers between years, it is important to standardize survey effort as much as possible. National surveys of the Rook *Corvus frugilegus* have been carried out in Britain from late March to late April.[1,2] The colony sites are usually traditional and used to a greater or lesser extent throughout the year, making them easy to locate and count.[3] The majority of nests are blown down in winter and rebuilt each spring, giving a good correlation with the number of breeding pairs present at the colony.[2]

However, no studies have quantified the changes in nest numbers during the breeding period and the implications for survey strategy. Therefore, a sample of colonies was monitored to test whether there was a single date on which colonies were at their maximum and if they showed predictable increases through time. This would clarify the effects of survey date upon nest counts. The effect of initial colony size on the synchrony of nest building and the number of nests added was also investigated.

METHODS

Colonies were defined as any group of nests more than 100 m from any other such group.[2,3] The survey transect sampled 18 roadside colonies, located in deciduous woodland, up to 15 km from Durham City, UK. Nest counts were made every 4 days between 1 April and 25 April 1996. The colonies had a range of sizes representative of the area, based on nest counts made in spring 1995 (range 5–136 nests, median 25, $n = 18$).

For the initial visit to each colony, the position of a nest was mapped by standing beneath it and measuring the distance to its nearest neighbour. For distances greater than 5 m, a tape was laid out under the colony, otherwise a metre rule was used to judge the distance. A note was also made of the nests built above one another. Where nests were tightly clumped, the decision as to how many nests were present was based on the intersection of the circular outlines. On subsequent visits, only nest losses or additions needed to be mapped onto these original plans of the colonies.

Nests were recorded as 'incomplete' (N_i) when light could be seen through the structure from underneath, or 'complete' (N_c) when this was not the case as the nest had been lined.[4]

Where it was possible to observe the nest-building activities of the Rooks during the surveys (at one colony the birds were too wary), it was noted that some N_i were inactive relict structures from the previous breeding season. In contrast, the N_c were all active from the first survey date with single Rooks or pairs

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recorded at the nest. Thus, the N_c criterion was used in the calculations as this was thought to be the best index of actual increases in the number of breeding pairs at the colonies through time.

Consistent decisions on compound nests and nest activity were aided by having only one observer throughout. Also, inaccurate counts due to access difficulties, large rookery size, nests in conifers and counts made from a long distance[2] were not a problem in this study.

To establish the statistical significance of the change in nest numbers over the survey period (Fig. 1), the N_c (and N_i) for each colony for each date was standardized by subtracting and then dividing by the initial N_c (or N_i) recorded for that colony on 1 April. The standardized N_c percentages were then arcsine-transformed before using a one-way ANOVA with Tukey's 'honestly significant differences' test[5] to identify significantly different means.

To determine whether colonies increased by the same proportion, the initial N_c for each colony was subtracted from the N_c recorded for that colony on the modal date of maximum counts. Thus, the time period over which the increases were compared was the same for each colony (Fig. 3).

Colonies were classified as 'small' (range 5–25 nests, median 18, $n = 9$) or 'large' (range 26–136, median 61, $n = 9$) if their maximum nest count during the survey period was less than or equal to, or more than the median of 25. Differences in the percentage increases and the dates of maximum counts between these two groups were investigated in SPSS (version 7.5.1) using the independent samples *t*-test and the Kolmogorov–Smirnov two-sample test, respectively. The independent samples *t*-test incorporates Levene's test for the equality of variances which is used to determine the *t*-test performed.

RESULTS

The pattern of nest change was the same across all colonies (Fig. 1). There was a significant difference in N_c between survey dates (ANOVA $F_{5,102} = 2.30$, $P = 0.003$). The Tukey test showed counts on 5 April were significantly lower than the last three survey dates at $P = 0.05$, with no significant increases after 9 April 1996. N_i showed an opposite trend over the same period, although the difference between the two measures is mainly due to some nests being started and completed between surveys with no N_i stage being recorded. Also, the fine-scale mapping showed that some N_i from the winter period remained until much later in the survey when they were completed or disappeared. Similarly, some N_c fell to the ground or returned to an incomplete state before disappearing.

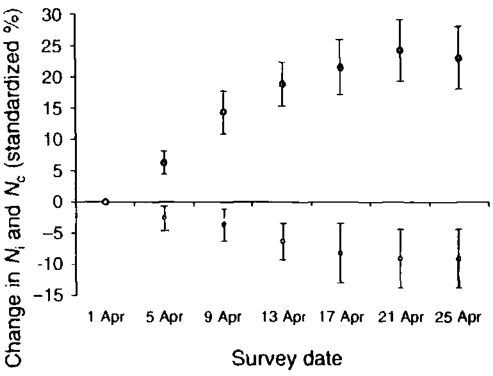

Figure 1. Change of N_i (O) and N_c (●) as standardized mean (± se) percentages of initial counts, for the survey period in April, 1996. The initial totals of N_i and N_c for the 18 colonies on 1 April are 36 and 643, respectively.

Colonies were asynchronous in reaching their maximum nest counts and no single date encompassed all colonies at their maximum. Most colonies (78%) were at their maximum on 21 April and 39% first peaked at this time (Fig. 2). There was no significant difference between small and large colonies with respect to the dates on which they first reached their maximum number of nests (Kolmogorov–Smirnov two sample test $D_{9,9} = 0.471$, $P = 0.979$).

Colonies increased significantly from their initial counts up to the modal date of maximum counts on 21 April across the range of colony sizes (Spearman rank correlation $r_s = 0.79$, $P < 0.01$; Fig. 3). The percentage increases at small colonies did not differ significantly from those at larg' colonies (independent samples *t*-test assuming unequal variances $t = -0.876$, df = 8.532, $P = 0.405$), although small colonies were more variable (range 0–80%) than large colonies (range 13–30%) (Levene's test $F_{1,16} = 15.04$, $P = 0.001$). The overall mean percentage increase up to 21 April was 24%.

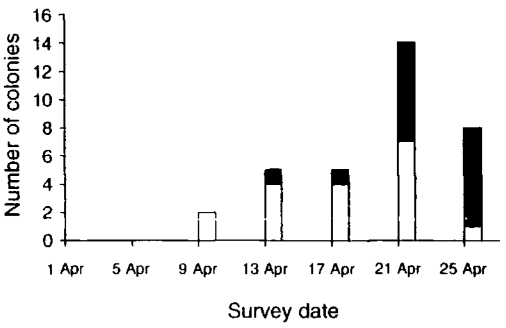

Figure 2. The survey date on which colonies first reached their maximum N_c and the number of colonies sustaining this count. (■) At maximum; (□) first at maximum.

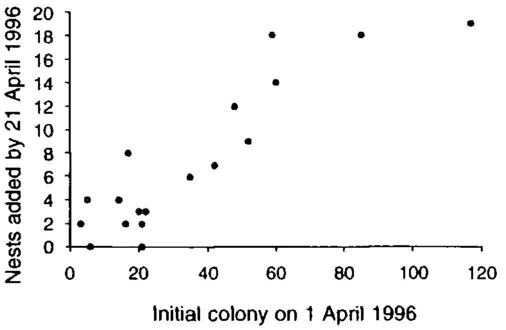

Figure 3. The increase in N_c recorded on 21 April (the modal date of maximum nest numbers) compared with the initial counts on 1 April.

DISCUSSION

This study examined the dynamics of nest numbers in Rook colonies from early to late April 1996, covering the weeks recommended for survey.[1,6] Some nests may be built in February, although most nesting activity begins in March,[7-9] as was noted leading up to this study.

The significant increases in colony size until the second week of April suggest that comparison of counts between years should consider only those made within the asymptote period after 9 April. If not, as in Brenchley's study[2] where counts from late March and early April were used to make inferences on how the rook population had changed, a correction factor should be applied. The present study shows that colonies may be at 80% or less of their potential maximum size at this early stage, and thus errors in comparisons with historical survey data may be considerable. The application of correction factors would go some way to overcoming this problem, although this assumes a common pattern of nest increase between years. Previous work suggests this may not be the case, as weather conditions preceding the breeding season can affect the build-up of nest numbers and would need to be taken into account.[9]

The problems for spatial and temporal comparisons of nest counts caused by a span of survey dates coupled with the effects of 'early' or 'late' springs and possibly latitude[10] could be tackled by repeating counts at a small number of colonies. Once counts in the sample have reached an asymptote, the additional colonies in an area can be counted. This would minimize the effect of 'early' and 'late' seasons and is preferable to a subjective assessment as suggested by Harris and Forbes for Shags *Phalacrocorax aristotelis*.[11] In volunteer surveys, the calibration of early counts using correction curves fitted to the sample colony data is probably more realistic considering the degree of co-ordination that would be required. Later counts may also need correction because of declines, although counting is usually precluded by leaf growth during May.[12] This decline may have started in the present study, although the decrease from 21–25 April was not a significant departure from the asymptote.

The percentage increases varied significantly more at small than large colonies, a tendency also exhibited in the dates colonies first reached their maximum counts (small, range 9–25 April; large, range 13–21 April). Both parameters suggest that smaller colonies (< 25 nests) may be less synchronous than larger ones (< 25 nests) across the area – as shown in the Gull-Billed Tern *Gelochelidon nilotica*[13]. This may be due to the effect of colony size on the sensitivity of the measures used, especially in the case of percentage increase.

The approximately linear relation of nest increases to colony size suggests colonies are not recruiting directly from a population of non-breeders during the breeding season. If non-breeders sampled and chose between many colonies, the relationship would probably be skewed by differential attraction effects. Instead, it is likely that non-breeders are recruited to breeding colonies before the breeding period, possibly during the previous breeding season, and remain associated with the colony throughout the year.[14] They may then start nesting according to their own thresholds for certain environmental cues, with the probability distribution for nesting over the April period simply scaling up from small to large colonies. The increase in social stimulation associated with increasing colony size may act to co-ordinate this pattern of nest establishment across the larger colonies.[13,15]

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