1. Introduction

1.1 Literature Review

The twite (*Carduelis flavirostris*) is a small graniverous finch which exhibits a disjunct population distribution across the Palaearctic regions of the world (BirdLife International 2004, Brown *et al* 1995, Davies 1988, Ellis 2004, Gibbons *et al* 1993, Langston et al 2006, McGhie *et* al 1994, Raine *et al* 2009, Sharrock 1976, Wilkinson 2007, Wilkinson & Wilson 2010). Finches are divided into two main groups, the *Fringillinae* (chaffinch and brambling) and the *Carduelinae* (hawfinch, greenfinch, goldfinch, siskin, redpoll, linnet, twite, bullfinch and crossbill) (Newton 1967). The twite is most closely related to linnet and redpoll and together they have been considered by some authors to be a separate genus, *Acanthis* (Vaurie 1959).

There are 8-10 subspecies of twite: the nominate subspecies (*C.f. flavirostris)* breeds in Norway and the extreme north-west of Russia as far as the Kola Peninsula (Newton 1972, Thom 1986, Wilkinson 2007). The *C.f. pipilans* subspecies is considered endemic to Britain and Ireland (Raine 2006, Raine *et al* 2009, Thom 1986, Wilkinson 2007, Wilkinson & Wilson 2010). The remaining subspecies, constituting the majority of the world population, are found mainly on the cold steppes and mountains of central and south-west Asia (BirdLife International 2004, Davies 1988, Newton 1972, Wilkinson 2007). The European population is considered to be greater than 170,000 birds (BirdLife International 2004), fewer than half of the global population, with the British population (including Ireland) being estimated to be a relatively small component at around 10,000 pairs (Langston *et al* 2006).

1.1.1 Distribution, Abundance and Population Trends in Britain and Ireland

The Twite has maintained steady populations across much of its global range with the exception of Britain and Ireland where it has experienced a significant decline over the past 20 years (BirdLife International 2004, Gibbons *et al* 1993, Raine *et al* 2009). Twite in Britain and Ireland are included in the Red List of Birds of Conservation Concern 3 (Eaton 2009) on account of a “Historic decline in the breeding population” and “Severe breeding population decline over 25 years/longer term”. By far the largest proportion of British twite breed in the north and west of Scotland, particularly in the Hebrides (Davies 1988, Sharrock 1976, Gibbons *et al* 1993, Langston *et al* 2006) with a smaller concentration in the south Pennines. Over the past 40 years, like many bird species, twite numbers have declined substantially across most of southern Britain (Donald *et al* 2001).

In Ireland numbers have declined by 50% (Gibbons *et al* 1993, Raine *et al* 2009) and in parts of England they have declined by 80% (Raine *et al* 2009). The only significant remnant population in England breeds in the south Pennines. The estimated British population in 1968-72 was 20,000-40,000 pairs (Sharrock 1976), however, Gibbons *et al* (1993) produced a higher estimate of around 68,500 pairs in 1988-91. Table 1 presents a summary of the results from Sharrock (1976) and Gibbons *et al* (1993).

Years	**Present, no breeding evidence**		**Breeding evidence**		**All records**		
	Britain	Ireland	Britain	Ireland	Britain	Ireland	Both
1968-72	154	42	503	85	657	127	784
1988-91	231	28	420	32	651	60	711
% change					-0.9	-52.8	-9.3

Table 1 - Summary population figures and trends for twite in Britain and Ireland from 1968-72 to 1988-91 (Gibbons *et al* 1993)

Holloway (1996) described the twite's historic distribution between 1875 and 1900, illustrating the longer-term extent of the decline in the distribution of twite across the British Isles with a 36% decline in the number of counties in which the birds were recorded between 1875-1900 and 1968-72 (Table 2). At that time twite were recorded in every county in Scotland, most counties in Ireland and the majority of the northern half of England.

Period	**Probable breeding**		**Confirmed breeding**		**Combined**		
	Britain	Ireland	Britain	Ireland	Britain	Ireland	Both
1875-1900	0	3	45	24	45	27	72
1968-1972	3	2	32	9	35	11	46
Change					-10 -22%	-16 -59%	-26 -36%

Table 2 – Number of counties in which twite were recorded in 1875-1900 and 1968-72 (Holloway 1976)

The first dedicated national survey of breeding twite was carried out in 1999 (Langston *et al* 2006) producing an estimated breeding population of around 10,000 pairs, with a range of 6,293 to 14,586 pairs (95% confidence intervals). The relatively wide population range presented here probably arises from the difficulty in surveying twite, particularly in terms of establishing clear evidence of breeding (Clark and Sellars 1998b, Gilbert *et al* 1998) and the fact that twite are not routinely monitored due to their patchy distribution

(Langston *et al* 2006). However, the survey clearly illustrates a continuing decline in range and numbers, particularly in Shetland, Orkney, Harris, Lewis, inland mainland Scotland and the south Pennines of England, the Pennines trend being further supported by a study by Raine *et al* (2009).

Given this ongoing decline and the fact that the endemic subspecies *C.f. pipilans* is one of a very few British breeding passerines whose population is of international significance, (Mearns 2009) research into twite biology and breeding ecology has been surprisingly limited, with the majority of work being focused upon the south Pennines population.

1.1.2 Breeding Performance and Habitat Preferences

Twite breed mainly on heather moorland (Newton 1972, Orford 1973, Brown *et al* 1995), in small colonies (Langston *et al* 2006, Wilkinson and Wilson 2010) at the moorland edge associated with enclosed agricultural fields that they utilise to forage for seeds. In the south, nest sites can be as high as 300-450 m above sea level (Orford 1973, Brown *et al* 1995) while in the north and west they tend to be more low lying or coastal. In general terms birds tend to nest within 1½ - 2 km of the enclosed agricultural fields (Orford 1973, Raine 2006, Wilkinson and Wilson 2010). The preferred habitat type has traditionally been heather-dominated (*Calluna vulgaris*) moorland (Orford 1973, Brown *et al* 1995, Marler and Mundinger 1975, Raine 2006, Wilkinson and Wilson 2010) of medium height (25-36 cm) (Orford 1973) with various other vegetation types being utilised to a lesser extent. However, in recent years there has been a shift towards increased use of bracken (*Pteridium aquilinum*) (Brown *et al* 1995, Gowthorpe 2009). Twite have also been associated with reservoir overspill areas and river margins (Brown *et al* 1995) particularly early in the breeding season (Raine 2006). They usually avoid rush (*Juncus* spp.) flushes and improved or over-grazed pastures and burnt areas (Brown *et al* 1995, Raine 2006). In South Uist and Harris twite are strongly associated with moorland edge habitats close to machair meadows, with the majority of nests being found in loose clusters in heather, although some were located in young conifer shelter-belt plantations (Wilkinson and Wilson 2010). Nest sites are traditional, i.e. birds return to the same sites year after year (Wilkinson *pers. comm.*), and are mostly within 1.6 km of their forage areas (Figure 1).

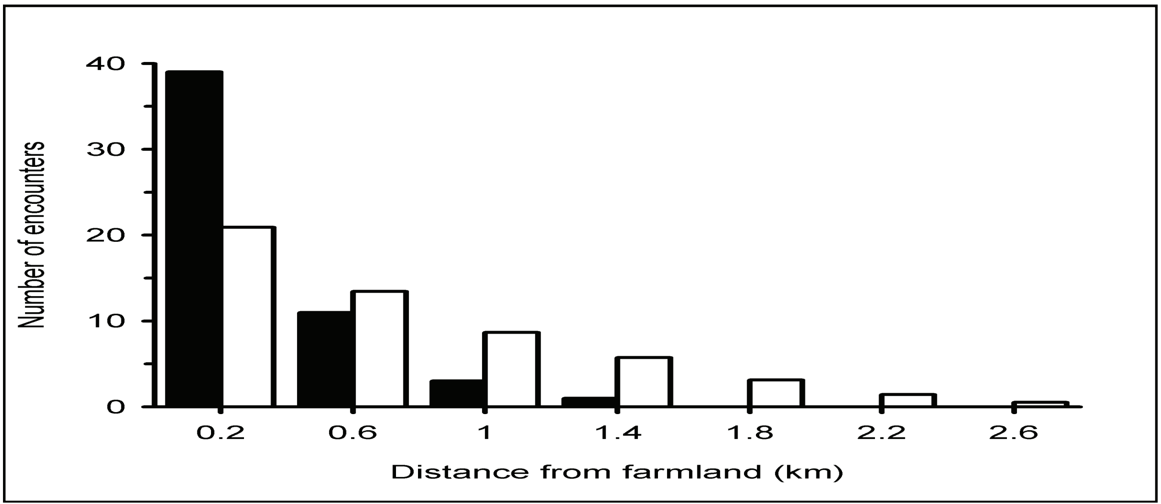

Figure 1 - Frequency distribution of breeding twite encountered on moorland in relation to the minimum distance from enclosed farmland, grouped by 400-m bins, from transect surveys in South Uist (2003-05) and South Harris (2005). Filled bars = observed; open bars = expected. (Wilkinson and Wilson 2010)

The twite's breeding season is largely defined by the period of maximum availability of their food and in general terms is shorter further north than in the south (Newton 1972). The beginning and length of the breeding season varies from year to year but is typically around May to mid-August with twite rearing 1-3 broods (Newton 1972, Orford 1973). Incubation lasts 11-13 days and the nestling period is 11-12 days (Newton 1972). Some birds will attempt a second brood prior to the first fledging (Marler and Mundinger 1975). In the south Pennines there appear to be fewer attempts at multiple clutches with few, if any, confirmed attempts in recent studies (Raine 2006) compared with some birds attempting up to three clutches in South Uist (Wilkinson & Wilson 2010).

Average clutch size is in the region of 5.0 to 5.5 across the country (Brown *et* al 1995, McGhie *et al* 1994, Raine 2006, Wilkinson and Wilson 2010). However, there is more variation in average daily nest failure rates, particularly at the nestling stage. In the south Pennines, Raine (2006) recorded average daily nest failure rates of 2.8% during incubation and 1.9% in the nestling stage, consistent with earlier figures from Brown *et al* (1995) and McGhie *et al* (1994). In South Uist and Harris the observed average daily nest failure rate was 1.3% during incubation and 0.4% during the nestling stage (although this latter figure was noticeably higher in one of the three survey years). In general terms the daily survival rates were higher in nests located within heather than in other vegetation types (Raine 2006). Breeding densities vary across the country (Langston *et al* 2006) with figures ranging from <5 to 250 pairs per 10 km^2 in Scotland, while in England the average was recorded at 154 pairs per 10 km^2.

1.1.3 Foraging Behaviour and Habitat Preferences

Twite feed on seeds of wild flowers and agricultural weeds which are often sourced a significant distance from their nest sites (Brown *et al* 1995, Langston *et al* 2006, Marler and Mundinger 1975, Newton 1972, Raine 2006, Reed 1995, Wilkinson & Wilson 2010). Their young are fed on regurgitated, undigested seed stored in the adult's gullet (Newton 1967). In Norway the key plant seeds were those of un-ripened dandelion (*Taraxacum vulgare*) and sorrel (*Rumex acetosa* and *Rumex crispus*) although there was some variation between different areas (Marler and Mundinger 1975). Table 3 summarises the seasonal preference of food plants in Norway with some limited observations from Ireland and Skye.

Species	Location	Date of Observation	Scattered (roadsides)	Clumped, common (pastures, cultivation)
Taraxacum vulgare *	Norway	6 Jun - 1 Jul		+
Rumex acetosa *	Norway	17 Jun – 17 Jul	+	
Rumex crispus *	Norway		+	+?
Epilobium angustifolium	Norway	5 Jul	+	
Carex spp.	Norway	6 Jul	+	
Deschampsia caespitosa	Norway	6 Jul	+	
Polygonum sp.	Norway	6 Jul	+	
Cerastium sp.	Norway	6 Jul	+	
Rumex spp.	Ireland	4 Aug		+
Hypochoeris radicata	Ireland	8 Aug	+	
Avena sativa *	Skye	19 Sep		+
Rumex spp.	Skye	17 Sep	+?	+
Centaurea scabiosa	Skye	18 Sep	+>	+

Note * = favoured forage

Table 3 – Favoured forage plants of twite during the breeding season (Marler and Mundinger 1975)

Twite avoid improved fields where livestock are present, apart from late in August when large numbers congregate to feed on thistle (*Cirsium*) seeds. Meadows are consistently selected by twite for foraging between May and August which is attributed to the abundance of dandelion and common sorrel (*Rumex acetosa*) which are key food plants (Raine 2006). Twite also use other habitats at certain times during the season, most notably dam overspills early in the season (April) and roadside verges which were an important source of flower seeds when the meadows had been cut (Raine 2006).

The timing of availability of these plant species is critical and explains an apparent foraging transition from one species to another, and sometimes from one foraging site to another, as the season progresses (Wilkinson and Wilson 2010). *Taraxacum* seed is only available for a limited period (c. 3 weeks) at the beginning of the breeding season, typically clumped in pastures or cultivated ground, after which the birds move onto *Rumex* which tends to be more scattered along the coast or roadsides (Marler and

Mundinger 1975, Raine 2006). Thus a succession of different plant seeds is required to meet the needs of twite throughout the breeding season (Figure 2).

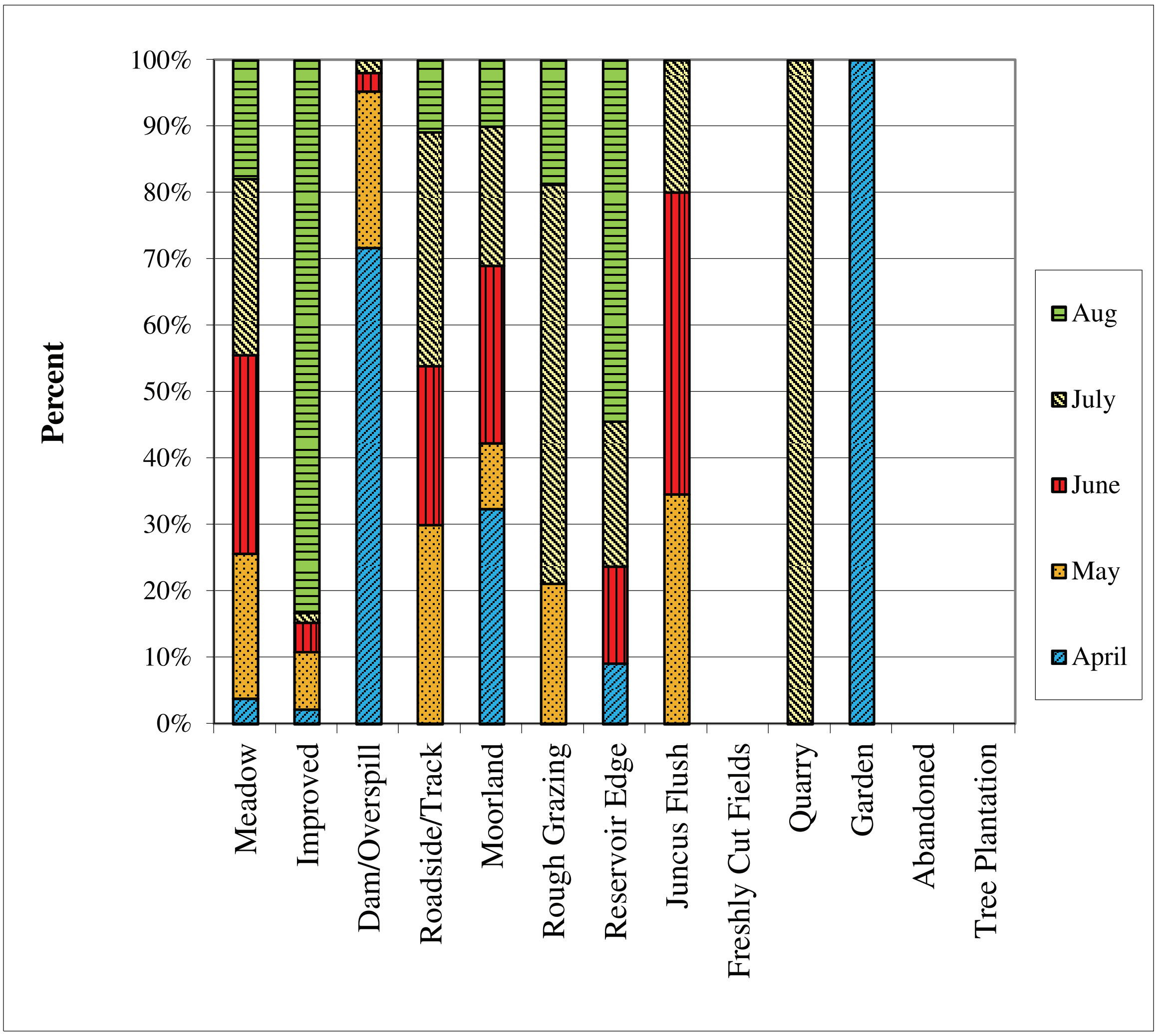

Figure 2 - Relative preference of different habitat types for foraging by twite in the south Pennines (Raine 2006)

In South Uist and Harris, twite demonstrate a similar seasonal shift in forage preference, related primarily to availability of different types of seed (Wilkinson and Wilson 2010). Figure 1 shows the seasonal variation in forage plants for twite in South Uist and Harris from 2003-05 illustrating the predominance of dandelion in the early season, declining to give way to common stork's-bill (*Erodium cicutarium*), blinks (*Montia fontana*), *Rumex* spp. and Autumn hawkbit (*Leontodon autumnalis*) as the season progresses. Seeds of grasses appear to be an important dietary component throughout the breeding season.

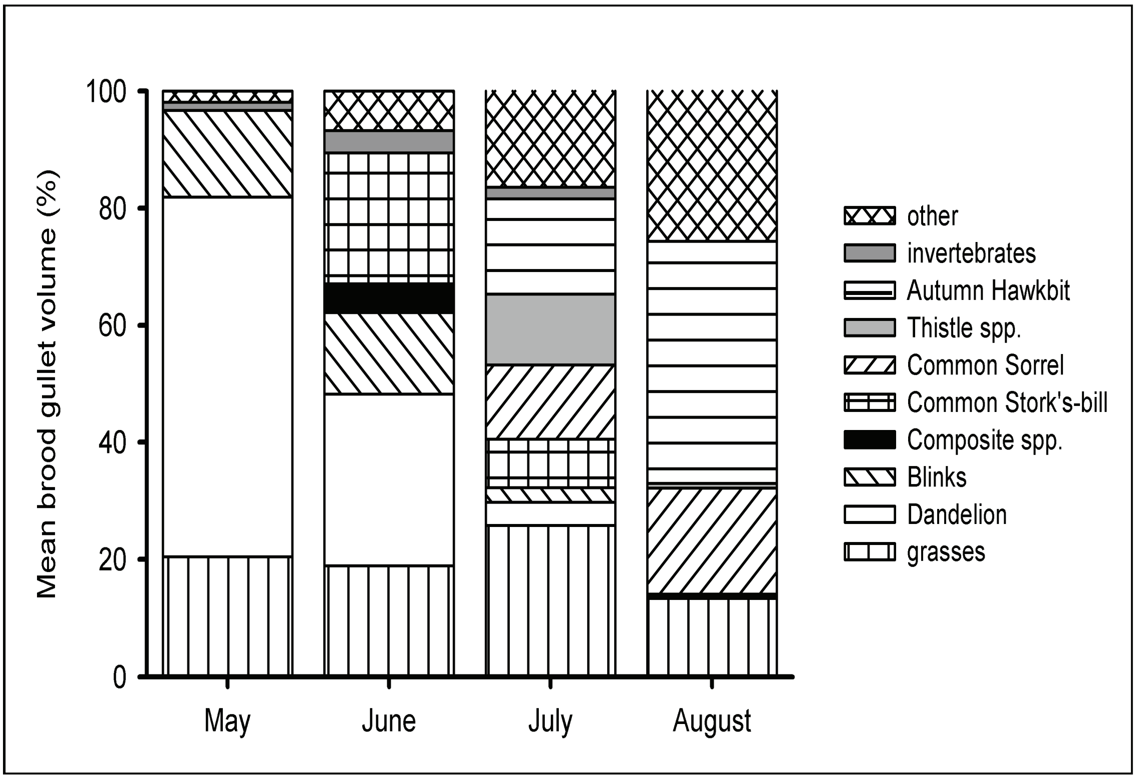

Figure 1 - Seasonal variation in diet composition of twite nestlings in South Uist in 2003-05. Data are presented as the mean percentage of brood gullet volume across repeat visits over all broods in that month for each seed type (May: n = 35; June: n = 68; July: n = 67; August: n = 22). Other = unidentified, partially digested and food types making up <1% of mean brood gullet volume. (Wilkinson & Wilson 2010)

Twite prefer a sward of medium height, allowing for easy movement and maximum availability of seed (Raine 2006). However, an overriding factor is the density of seeding wild flowers (Figure 2). Raine (2006) applied a 'flower score' to every meadow according to the percentage cover of wildflowers and this proved a useful predictor of twite presence, although only by predicting fields that twite would not use.

Thus, there is a complex mix of habitat requirements for foraging twite which varies throughout the season with different critical conditions at different times. The relative importance of these features is unclear, but presumably a combination of all would provide the optimum foraging habitat for breeding twite, and loss of any of these features might be expected to impact upon breeding success.

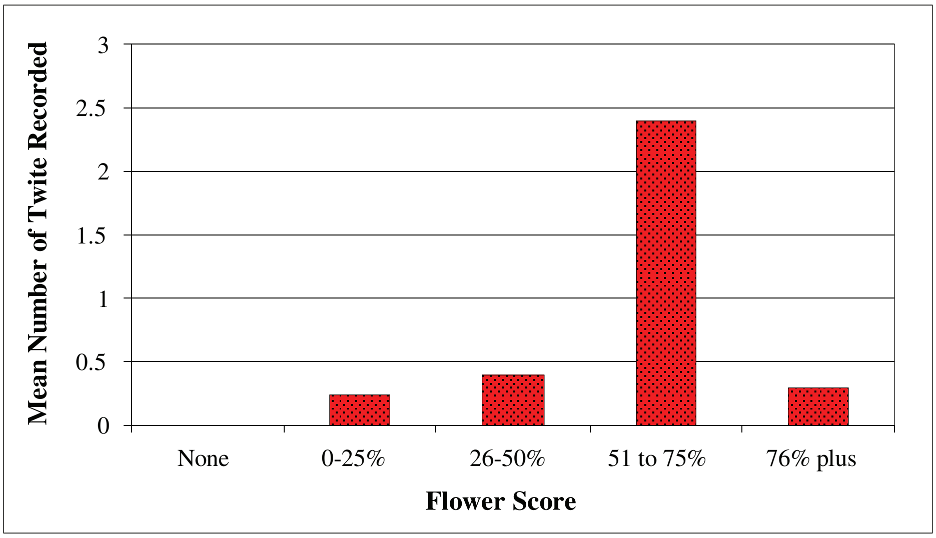

Figure 2 - Mean number of Twite recorded for fields in each flower score category (Raine 2006)

1.1.4 Migration and Wintering Habitat Preferences

Apart from the changes in habitat suitability at their breeding and foraging areas, twite have traditionally migrated, generally in a south-eastwards direction. Many of these wintering areas have also experienced significant changes over recent decades (Brown and Atkinson 1996, Clark and Sellars 1998a,1998b and 1999, Dierschke 2002, Hancock and Wilson 2003, Lack 1986, Mearns 2009). It is possible that these changes may be having an impact on survival rates, and hence on the population that returns to the traditional breeding sites. However, for the purposes of this study the wintering and migration habits and patterns of twite are of limited relevance. This study is concerned with the factors that influence breeding behaviour and success, hence these studies of wintering twite are not reviewed here.

1.1.5 Twite Conservation

Over the past 40 years agricultural practices have altered beyond anything experienced previously (Wilson *et al* 2009), including the intensification of grassland management, increased stocking on hill and moorland grazings. Traditional methods of cutting and stacking hay have all but disappeared, being substituted by silage production with earlier cutting dates and the loss of stubble fields as new crops are sown immediately following harvest in some areas. Drainage has improved land previously unavailable for cropping or pasture (Fuller 1982, Wilson *et al* 2009) resulting in a loss of rough margins, heather moorland margins and species-rich meadows. All of these changes will impact upon the availability of seeds for breeding twite to feed on (Langston *et al* 2006, Raine 2006, Wilkinson and Wilson 2010) and with associated burning practices and over-grazing, traditional nest sites have been lost, or at least degraded to the point where bracken is now a key species for nesting twite (Brown *et al* 1995, Raine 2006). Changes to wintering habitats may also be having an impact on survival rates (Brown and Atkinson 1996, Fuller *et al* 2002, Mearns 2009).

Brown *et al* (1995) concluded that modern agricultural and sporting estate management practices were detrimental to the survival of twite, primarily as a result of the loss of heather. Indeed heather-dominated moorland declined by 25% in Scotland and 20% in England and Wales between 1940 and 1980 which illustrates the scale of this problem (Sim *et al* 2005). Hence, the increasingly important role of bracken in twite breeding behaviour in the Pennines has possibly arisen from a decline in heather caused by burning of grouse moors and over-grazing by sheep (Orford 1973). This is probably a sub-optimal habitat for breeding and may partially account for the decline in numbers of breeding twite in the south Pennines as compared with the Western Isles.

In response to this decline, action is beginning to be taken to prevent further decline and encourage expansion of this internationally important species, including a raft of Species Action Plans (SAPs), the North-West Twite Project (Sowter 2006) and the English Twite Recovery Programme (Natural England 2009). These plans and programmes all focus on land management in the uplands, both at nesting sites and on farmland typically used by foraging twite to ensure the population does not decline further, and to expand suitable habitat with the aim of improving breeding success. Typical actions include protection and encouragement of bracken stands, to allow time for longer-term action to encourage regeneration of heather moorland, encouragement of appropriate cropping and grazing regimes on upland farms and monitoring of twite numbers and land use change (Gowthorpe 2009, Peak District Twite BAP 2000, Calderdale Council 2009, Greater Manchester Council 2009, Northern Ireland Twite SAP 2006, Sowter 2006).

In stark contrast to this action in the south, no Scottish Local Authority has as yet produced a twite SAP, with the possible exception of Shetland who have included plans for twite conservation as part of a wider strategy for arable birds (Ellis 2004). Given the relatively healthy condition of breeding twite numbers in north and west Scotland, it is surprising that there has been so little effort applied to ensuring that they do not follow the pattern recorded in the south over the past few decades.

1.1.6 Analysing and Modelling Species Distribution and Abundance

Analysis of species distribution and abundance is perhaps one of the most common tasks undertaken by conservationists, particularly those with an interest in species management. There has developed an extensive array of different methods of analysing these kinds of data (Fotheringham *et* al 2002, O'Sullivan and Unwin 2003, Rogerson 2001), often derived for specific purposes (Davis *et al* 2003). Given the obviously spatial nature of such data GIS can play a key and very valuable role in understanding patterns and relationships (Burrough and McDonnell 1998, De Mers 2003, Heywood *et al* 2006, Longley *et al* 2005, Longley *et al* 2005a, O'Sullivan and Unwin 2003, Scally 2006). As indicated in previous sections the amount of data available on twite distribution and especially abundance is limited, particularly in Scotland. In many cases either the resources, or data, available for conservation initiatives are limited (Bayliss *et al* 2003, Bayliss *et al* 2005) and hence scientists have resorted to using models to improve understanding of biological processes and plant and animal populations (Morain 1999). Models are used for many and varied purposes including simulation of processes, testing theoretical hypotheses, considering potential implications of different actions or decisions and creation of measures of suitability or sensitivity (Heywood *et* al 2006, Longley *et al* 2005). Such models allow investigations into possible responses to different scenarios as defined by selected parameters considered to be critical to the ecological processes involved. Often it would not be feasible to undertake lengthy research projects, and models offer the only viable method of studying some ecological processes (Brooks 1997).

Longley *et al* (2005) define models as an expression of how the world is believed to work, i.e. they are an expression of process. They suggest that models can be categorized into four key types:

1. *dynamic* – modelling processes such as erosion, typically involving the simulation of movement
2. *social processes* – modelling segregation, movement of vehicles along a road, etc.
3. *optimisation* – modelling processes designed by humans to look for optimum solutions, e.g. best location for a shop or factory.
4. *indicators or predictors* – combination of layers of geographic information to derive an overall indication or prediction of a given outcome.

The fourth type is the most relevant to the study of twite and their nesting and foraging habitat preferences. This kind of model is typically known as a Habitat Suitability Index (HSI) model and they are commonly used in environmental management and conservation (Brooks and Temple 1990, Brooks 1997, Donovan *et al* 1987, Elith *et al* 2008, Hirzel *et al* 2002, Hirzel and Arlettaz 2003, Hirzel *et al* 2006, Johnson 2007, Larson *et al* 2003, Larson *et al* 2004, Store and Jokimaki 2003, Store and Kangas 2001).

Models can range in complexity (Potts and Elith 2006) from the relatively simple Generalised Additive Models (GAMs) and Multiple Criteria Evaluation (MCE) which combine a number of factors by summing their values with or without weighting (Bayliss *et al* 2003), to more complex combinations (Brooks and Temple 1990, Samu 2008), to highly complex statistical models such as Boosted Regression Trees (BRTs) based on derived relationships between parameters and the variation between the predicted values and actual data (Elith *et al* 2006, Elith *et al* 2008, Schonlau 2005, Townsend Peterson *et al* 2007). These models can be very powerful management and planning tools, but in essence modelling consists of combining many stages of transformation and manipulation into a single step for a single purpose (Longley *et al* 2005). Thus a series of different processes or events can be brought together to simulate a complex interaction of factors to estimate or predict an outcome.

For a model to have any value it must be calibrated against real data to determine appropriate values for its parameters and to ensure that the rules are valid. Good models can be tested for validity to ensure they give a good representation of reality (Bender *et* al 1996, Fielding and Haworth 1995, Lauver *et al* 2002, Leathwick *et al* 2006, Manel *et al* 2001, Morain 1999, Segurado and Araujo 2004, Vaughan and Omerod 2005). Typically this is achieved by cross-validation, whereby a random sample of the data that might have been used to derive the model originally, is instead reserved to test the model once it is complete (Longley *et al* 2005). This can be done by applying the model to data from either another time or another area, but care must be taken to ensure that conditions are comparable at each time period or area. Good models should also be transparent, i.e. the purpose of the model, its assumptions and parameters and relationships are clear to the user (Morain 1999) which requires clear and readily accessible documentation.

Since models can only be approximations of reality, any output should be accompanied by a realistic measure of the uncertainty associated with the result (Longley *et al* 2005, Morain 1995). How sensitive is the model to variations in each of the input parameters?

How sensitive is the model to errors in the weighting of each parameter? Is the output meaningful and does any labelling of outputs convey the correct message (Longley *et al* 2005)?

1.1.7 The Role of GIS in Analysis and Modelling of Species Distribution

The development of models can be broken down into a number of stages and GIS offers a huge range of options for each stage including the use of queries, measurements of spatially variable data, manipulation and transformation of data, description and summary of complex data, optimisation of site selection, e.g. maximum habitat suitability, and hypothesis testing (Heywood *et al* 2006, Longley *et al* 2005). As such GIS is used increasingly as an integral part of the development of models for species distribution and abundance (Brooks and Temple 1990, Gibson *et al* 2004, Green and Stowe 1993, Larson *et al* 2003, Meyer *et al* 2007, Phua and Minowa 2005, Store and Jokimaki 2003, Suarez Seoane *et al* 2002).

Many GIS software packages now include the capacity to develop integrated models, and certainly all have some of the tools required to undertake the various stages of model development. Within the ESRI ArcGIS software there is a specific tool that allows the user to develop a model that essentially brings together a series of tasks into a single command or tool (ESRI 2006, ESRI 2006a). This tool requires the developer to undertake the assessment of which parameters are critical to the process being modelled, and how these factors interact. However, utilising the wide range of analytical tools available within ArcGIS's Spatial Analyst toolbox it is possible to combine traditional statistical analysis with more spatial or geographic elements, such as elevation, slope and aspect, proximity and intersection or overlay, combining datasets that share no features other than relating to the same location. This capacity greatly increases the power of the model, particularly in the context of ecological processes.

However, as with all models, the results of running a model are only as reliable as the quality of the data used for the analysis and the accuracy of the assumptions and rules upon which the model is based. Thus the process of model development is critical, including the use of appropriate data and the assessment of relationships and interactions between critical factors.