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Natal philopatry and local movement patterns of Twite *Carduelis flavirostris*

ANDRÉ F. RAINE[1]*, DAVID J. SOWTER[2], ANDREW F. BROWN[3] and WILLIAM J. SUTHERLAND[1]
[1]Centre for Ecology, Evolution and Conservation, School of Biological Sciences, University of East Anglia, Norwich NR4 7TJ, UK [2]5, The Grove, Penwortham, Preston, Lancs PR1 0UU, UK [3]English Nature, Northminster House, Peterborough PE1 1UA, UK

The Twite *Carduelis flavirostris* is classified as a red-listed bird of conservation concern in the United Kingdom. Successful conservation initiatives will depend on an understanding of local movement patterns and natal philopatry as these will be important in determining how likely the species is to colonise new nesting areas. Natal philopatry was studied in twelve breeding colonies in the South Pennines Special Protection Area using an intensive colour-ringing programme. Of twenty birds colour-ringed as nestlings and relocated in a subsequent breeding season, half had returned to their natal colony. Seven had moved to adjacent colonies while the remaining three had moved up to 12.1 km away. Local movement patterns were studied by colour-ringing birds at two feeding stations outside the breeding season. These birds did not necessarily breed in adjacent colonies in subsequent years but rather dispersed throughout the South Pennines. In the post-breeding season, before winter migration, adults and first-year birds moved extensively throughout the study area. During this time, certain key feeding sites were utilised by individuals from widely dispersed colonies. The observed pattern of natal dispersal and local movements within the South Pennines suggests that historical breeding sites can be recolonised if appropriate breeding conditions are restored.

The Twite *Carduelis flavirostris* is currently classified as a red-listed bird of conservation concern in the United Kingdom, with a breeding population estimated at 10,000 pairs (Gregory *et al* 2002, Langston *et al* 2006). The majority breed in Scotland, with small populations in England, Ireland and Wales (Newton 1972). In England, the most important population, of approximately 200 breeding pairs, is located in the South Pennines Special Protection Area (SPA) (Batty *et al* 1999, Raine 2006).

This species' breeding range has contracted markedly in historic times with the recent decline being particularly widespread and rapid (Gibbons *et al* 1996, Brown & Grice 2005). Obtaining detailed information on its ecology is therefore important if attempts to restore its range and numbers are to be successful. Data on natal philopatry and site fidelity are especially valuable, particularly when considering how likely the species is to recolonise areas from which it has been lost (Saunders *et al* 1991, Fahrig & Merriam 1994). For example, in colonially breeding species and many raptors, strong site fidelity will result in individuals occupying only a portion of the breeding habitat available (Matthiopoulos *et al* 2005). If this is the case with Twite, then the likelihood and speed of recolonisation might be lower than expected.

Natal philopatry and site fidelity have been studied in a diverse array of passerines. The general pattern is of site faithfulness in adults, but a degree of dispersal in first-year birds (Greenwood 1980, Greenwood & Harvey 1982). A second general pattern is that females usually disperse further than males (Greenwood *et al* 1979, Greenwood & Harvey 1982). Dispersal distances are often larger in younger birds due to competitive exclusion by adults for either territories or breeding opportunities (Badyaev & Faust 1996, Lozano & Lemon 1999). Other factors which may have an impact on natal dispersal distance include inbreeding avoidance (Shields 1984, Charlesworth & Charlesworth 1987), site availability and mate choice (Steiner & Gaston 2005), overall species abundance and size of geographical range (Paradis *et al* 1998). Migratory species often have lower instances of natal philopatry (Gauthreaux 1982), possibly because they leave natal areas in the winter and are therefore less familiar with their natal areas than resident species (Weatherhead & Forbes 1994).

Twite in the South Pennines breed colonially, with pairs nesting in close association with each other (Raine 2006). The only information currently available on natal philopatry of Twite breeding in the UK is a bird initially ringed as a nestling in the South Pennines and relocated breeding 6 km from its natal colony (Brown & Atkinson 2002). The aim of this study was to consider natal philopatry in Twite to ascertain whether restored and appropriately managed habitats have the potential to be

*Correspondence author
Email: andre.raine@uea.ac.uk

recolonised by breeding birds. The geographical targeting of habitat restoration projects will depend greatly on the strength of natal philopatry in this species. Localised movement in both the pre- and post-breeding periods have also been examined.

METHODS

Study area

A colour-ringing study was undertaken in the South Pennines Site of Special Scientific Interest in northwestern England (an area of approximately 250 km² centred on 53°28'N, 01°45'W). Twite were ringed as nestlings at twelve different breeding colonies within the South Pennines study area. These colonies varied in size from six to 50 pairs. Birds were also captured at two baited feeding stations provisioned with niger *Guizotia abyssinica* seed. Each station consisted of a cleared area of ground (approximately 2 m²), with 700 g of niger added every other day throughout the year. Feeding stations were 12.6 km apart, with one in Lancashire (Cant Clough Reservoir, grid reference SD8931) and one in Yorkshire (Light Hazzles Reservoir, SD9619). The provision of supplemental food was unlikely to have any effect on breeding behaviour, since birds stopped using supplemental food in preference to natural food sources during the peak breeding months of May and July (Raine 2006).

Colour-ringing scheme

Between 2002 and 2005, 342 Twite nestlings were individually colour-ringed with two coloured plastic rings on the left leg and a third colour ring placed above or below a metal British Trust for Ornithology (BTO) ring on the right. Fewer nestlings were ringed in 2005 due to a reduction in nest-searching effort because of other fieldwork priorities. A further 1,703 Twite were caught and ringed at the two feeding stations, using whoosh nets and mist nets (Table 1). Birds either were given individual combinations (using the same scheme as the nestlings), or were allocated cohort combinations with year- and site-specific combinations (consisting of two colour rings signifying date and site of capture on the left leg and a metal BTO ring on the right).

The authors and local birdwatchers searched for colour-ringed breeding birds in all known colonies throughout the South Pennines SPA during intensive surveys each year. In addition, the authors were alerted to the locations of all Twite found during a systematic constant-search-effort survey of the entire SPA conducted in 2004 and 2005 (Carr & Middleton 2004, Raine 2006) and were thus able to survey the few colonies which would otherwise be unknown to us. Birds were considered to be breeding at a site if nests were located or if they were recorded exhibiting breeding behaviour, defined by Gilbert *et al* (1998) as: (i) flight displays over suitable nesting habitat, (ii) birds carrying nesting material into suitable nesting habitat, (iii) the presence of distinct pairs, (iv) the presence of recently fledged young, (v) agitated behaviour at a potential nest site, or (vi) a bird reluctant to leave an area where flushed (often circling the surveyor and making alarm calls). Birds were considered to have returned to their natal colony if they were relocated displaying breeding behaviour within a radius of 1.5 km from their original nest site.

Table 1. Number of birds ringed between 2003 and 2005 at breeding colonies and feeding stations in the South Pennines. The numbers in brackets adjacent to totals indicate number of individual ring combinations used.

Site	2003	2004	2005	Total
Feeding stations				
Lancashire (Cant Clough)	546	247	167	960 (56)
Yorkshire (Light Hazzles)	335	176	232	743 (117)
Colonies				
Nestlings	152	165	25	342 (342)

To assess post-fledging dispersal and localised movement patterns, colour-ringed birds were searched for throughout the South Pennines SPA by the authors and local bird-watchers. This allowed the study to cover effectively the vast majority of potential feeding areas within the South Pennines SPA.

Statistical analysis

General statistics were carried out using SPSS version 11.0 (SPSS Inc, Chicago, USA). Where means are given, these are presented with standard errors. As the majority of the data sets were not normally distributed, non-parametric statistics were used in most cases throughout the paper. Where non-parametric statistics were used, medians are presented alongside means and standard errors.

RESULTS

Natal philopatry

Twenty birds ringed as nestlings were relocated exhibiting breeding behaviour in a subsequent breeding season (Fig 1). Of these, 10 had returned to their natal colony to breed. Of the remainder, seven had moved to adjacent breeding colonies within 5 km, one had moved 8.6 km and two had moved over 10 km from their natal colony. The mean dispersal distance was 2.5 ± 0.9 km (median = 0.7 km), with a maximum dispersal distance of 12.1 km. The

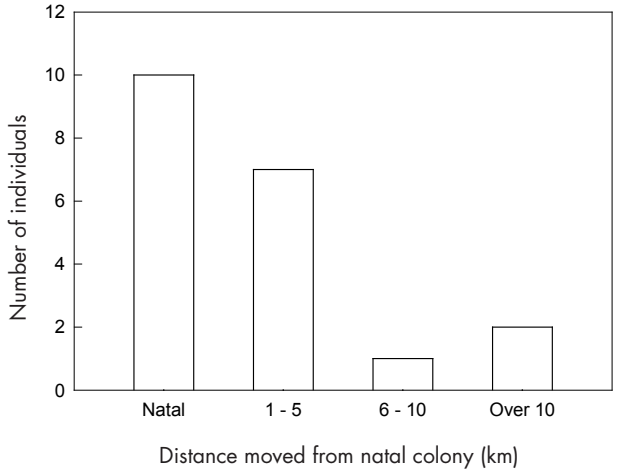

Figure 1. Distance (km) moved by birds ringed as nestlings from natal colonies to known breeding sites (n = 20).

mean natal dispersal distance of males was 0.8 km ± 0.5 (median = 0.0 km), while for females it was 2.3 km ± 1.0 (median = 1.9 km), but this difference was not significant (Z =1.45, df = 10, $P > 0.05$).

Dispersal of birds from feeding stations to breeding sites

Where sex was positively identified, 58 males and 41 females ringed at the two main feeding stations were subsequently identified by their colour rings on nest sites within the study area. They were distributed over all the breeding colonies surveyed in the South Pennines study area (Fig 2). The furthest distance moved from ringing to breeding site within the South Pennines was a female ringed at the Lancashire site and resighted at a colony 28.8 km away.

There was no significant difference (Z = 1.03, $P > 0.05$) between sites for the distance birds moved from ringing site to breeding site (Lancashire feeding station, n = 58, mean 7.4 km ± 0.9, median 2.1 km; Yorkshire feeding station, n = 41, mean 4.1 km ± 0.4, median 2.9 km). There was also no significant difference (Z = 1.48, $P > 0.05$) for the distance moved by either sex between ringing site and breeding site (males, n = 51, mean 6.9 km ± 0.8, median 2.9 km; females, n = 48, mean 5.1 km ± 0.8, median 2.9 km).

The number of colour-ringed birds in the breeding population was high, with 50.4% (n = 145) of all known breeding birds at colonies being colour-ringed. However, these were not evenly spread throughout the study area. Colonies adjacent to ringing sites contained a higher proportion of ringed birds than those that were farther away. For example at Cant Clough, which is only 2.1 km from a ringing site, 92.9% (n = 56) of birds seen in the

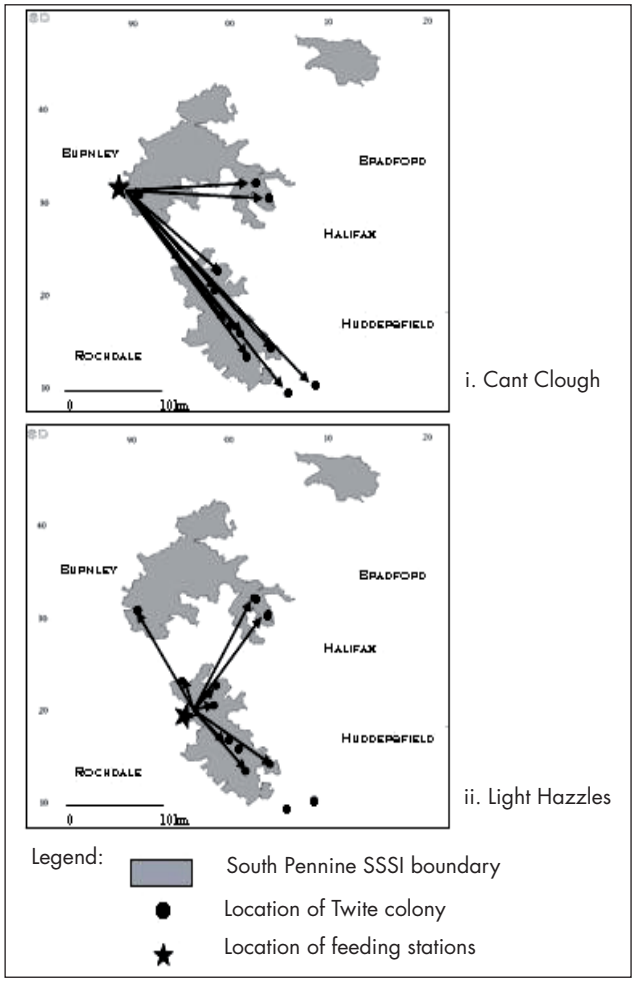

Figure 2. Maps showing movement of birds ringed at (i) Cant Clough feeding station, Lancashire (n = 79) and (ii) Light Hazzles feeding station, Yorkshire (n = 48) to confirmed breeding sites.

breeding colony over the study period were colour-ringed, whereas at Wessenden, which is 14.8 km from the closest ringing site, only 12.5% (n = 8) of breeding birds were ringed. Unringed breeding birds were significantly (Z = 8.17, $P < 0.0001$) further (5.9 km ± 0.3, median = 4.0 km) away from the nearest ringing site than ringed breeding birds (3.5 km ± 0.2, median = 2.4 km)

Post-fledging dispersal

In all, 146 nestlings (42.3%) from 58 nests (77.3%) were resighted after fledging. In the post-fledging period up until first winter migration, the mean number of days to first resighting after fledging was 75.4 ± 2.8 days (n = 103, min = 16, max = 123). The period between fledging and winter migration was split into three 40-day periods to ask whether the distance moved varied in relation to time after fledging. Of 29 birds resighted in the first 40 days after fledging, the mean distance moved was 1.4 km ± 0.2 (median = 1.7

km) from the nest site. Distances were significantly (χ^2 = 46.50, $P < 0.0001$) greater in the next 40-day period (4.8 km ± 0.6, median = 2.1 km, n = 89) and the final 40-day period before winter migration (6.8 km ± 0.7, median = 2.7 km, n = 108).

Of 131 nestlings resighted in the post-fledging period up until winter migration, 88 (65.2%) were recorded making movements of under 5 km from their natal colony (Fig 3). The mean distance moved by birds between fledging and first winter migration was 7.3 km ± 0.7 (min = 1.4 km, max = 46.0 km, median = 2.6 km). Larger movements consisted of newly fledged birds moving to several sites outside their natal colonies, indicating extensive localised movement by newly fledged birds. The mean time it took pulli to make localised movements over 10 km before first winter migration commenced was 88.1 days ± 3.2 (median = 96 days). Much of this movement was undertaken by birds moving to the two main feeding stations (although birds also utilised traditional upland meadows and reservoir edges throughout the study area). Individuals also moved on a regular basis between feeding stations (a distance of 12.6 km): 38.2% of all nestlings were recorded moving between the two feeding stations at least once. Over the course of the study, 14 individuals moved between stations twice, five individuals three times, one bird four times and one bird a total of seven times.

Localised movement patterns

During the pre- and post-breeding periods, there were significant localised movements within the study area. Of all birds ringed at the Lancashire feeding station, 6.2% (n = 50) moved at least once to the Yorkshire feeding station. Likewise, 3.9% (n = 27) of all birds ringed at the Yorkshire feeding station were resighted at least once at the Lancashire site. Of these individuals, 13.7% moved between stations at least twice. Twite were also resighted at eleven locations outside the two main catching sites. These were typically reservoirs or flower-rich hay meadows. The mean movement to these sites was 13.4 km ± 0.7 (n = 41, min = 2.3 km, max = 26.3 km, median = 13.4 km) (Fig 4).

DISCUSSION

Natal philopatry and breeding dispersal

This study involved the intensive survey of the vast majority of remaining Twite breeding colonies in the South Pennines SPA. This project was heavily publicised to generate as much coverage of the breeding grounds as possible and involved not just the authors but large numbers of local birdwatchers and included reports from teams of professionals surveying the SPA for breeding birds. Therefore, we consider coverage of the SPA to have been very thorough. Consequently, we believe that our estimates of dispersal distances within the South Pennines SPA are robust and were not constrained by search efforts.

Half of all resighted birds ringed as nestlings returned to natal colonies to breed. The remaining birds dispersed elsewhere, with several breeding a substantial distance away from the natal site. The mean (± sd) natal dispersal of Twite (2.5 km ± 3.8) was lower than that for several other *Carduelis* finches (Paradis *et al* 1998): Greenfinch *Carduelis chloris* had an mean (± sd) natal dispersal of 4.2 ± 6.4 (n = 99), Linnet *C. cannabina* 4.4 ± 8.8 (n = 147), Goldfinch *C. carduelis* 11.1 ± 18.2 (n = 85) and Mealy Redpoll *C. flammea* 22.7 ± 31 (n = 31). This could simply be due to a smaller sample size or different methodologies. However, these differences

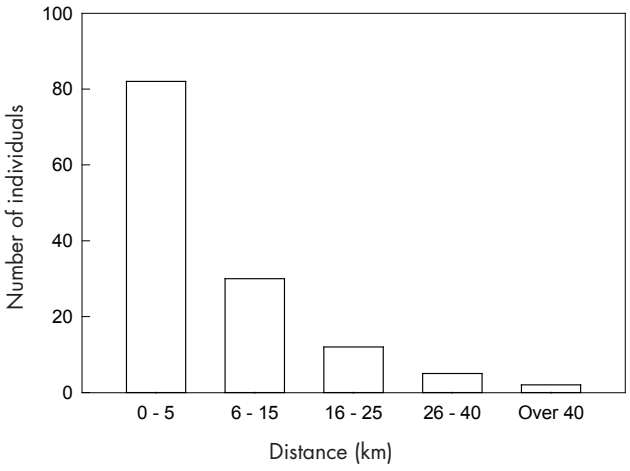

Figure 3. Cumulative distance (km) moved in the post-fledging period before first winter migration by Twite ringed as nestlings (n = 131).

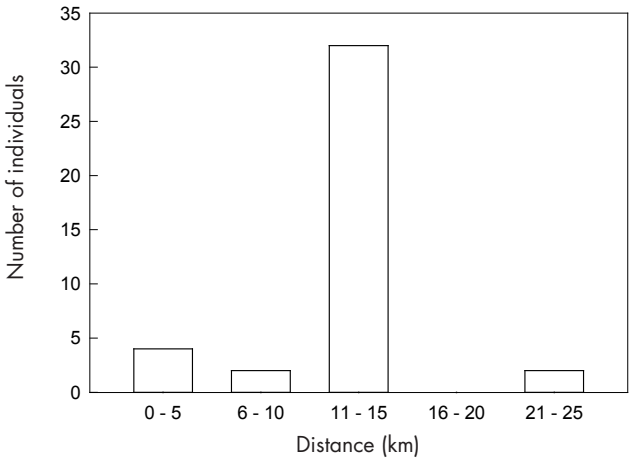

Figure 4. Distance (km) moved outside the breeding season by Twite ringed at two feeding stations (n = 41).

could also be related to breeding ecology. Neither Redpoll, Goldfinch nor Greenfinch nest colonially, whereas the Twite (and Linnet) are semi-colonial (Newton 1972). Natal dispersal is often greater than breeding dispersal in passerines because first-year birds can be excluded from sites by resident adults as they may be less competitive for breeding territories or partners (Greenwood 1980, Badyaev & Faust 1996, Lozano & Lemon1999). However, as male Twite defend the female as a mobile territory and do not have a traditional physical territory (Marler & Mundinger 1975), exclusion by adults is less likely to be of significance.

Natal dispersal did not differ significantly between the sexes, as it does in many passerines (Greenwood & Harvey 1982). This was also true for the distances moved by males and females ringed at feeding stations and relocated at nest sites. Female dispersal in birds is also often due to male territory establishment (Greenwood 1980). Again, the semi-colonial breeding ecology of the Twite may reduce this effect.

Birds ringed at feeding stations in the pre- and post-breeding periods were also capable of large dispersal movements, with birds found breeding at colonies distributed throughout the study site. Furthermore, two individuals ringed in the South Pennines at feeding stations were resighted outside England in circumstances which we believe strongly indicated breeding in those areas (Raine *et al* 2006). One individual was ringed on 26 July at the Lancashire feeding station and was resighted in late July the following year in a family party on Sanda, Scotland. The second bird, ringed in the post-breeding period at the Lancashire site, was resighted on 30 July the following year on Snowdon, Wales. As the Scottish breeding record involved a bird originally ringed in the South Pennines in July, long before winter migration began, it was almost certainly a bird hatched in the South Pennines.

These movements show that Twite are capable of dispersing considerable distances, and this has important implications for conservation. Many known colonies, both within the South Pennines and elsewhere, have been abandoned in recent years. Twite populations in the South Pennines have thus become highly fragmented and localised (Batty *et al* 1999). As birds are capable of dispersing over large distances they could potentially recolonise such sites if they were managed in a manner sympathetic to their breeding requirements.

Local movement patterns

The majority of newly fledged birds resighted during the first few weeks after fledging were found in the vicinity of the nest site, where they were still being fed by adults. They remained hidden in tall heather or dense bracken, which may help to explain the importance of older bracken stands and taller vegetation in nest-site selection. Subsequently they dispersed over wide areas, often gathering at abundant food sources. Furthermore, individuals were not restricted to a single feeding area, with many actively utilising several feeding sites, in some cases located up to 12.6 km apart. Movement between these sites often occurred on a regular basis with birds moving up to 31.5 km over the course of the post-breeding period. It has been suggested that large post-fledging movements may serve an important role in locating future breeding or overwintering sites (Baker 1993).

This pattern of localised movement and the utilisation of several food sources was also noted in birds ringed at feeding stations. Flocks utilising these sites were found to have a significant turnover rate, with the same individuals often being found at both the Lancashire and Yorkshire sites during the post-breeding period. This type of foraging behaviour allows birds to take full advantage of potentially ephemeral food sources.

These movement patterns have several important conservation implications. Firstly, they demonstrate that flocks that build up at key feeding areas (both feeding stations and natural food sources) do not necessarily come from adjacent breeding colonies. Therefore, large flocks of Twite at these times do not necessarily indicate that there are breeding colonies nearby but instead may be composed of birds from widely spread colonies. This catchment area is extensive, as indicated by the appearance of colour-ringed birds from as far as 28.2 km away. If supplemental feeding stations are to be part of a conservation initiative, a few carefully placed stations could be beneficial to birds breeding in a wide area. The same is true for natural feeding areas. In late July and August, Twite were often found to concentrate in a few locations; either in traditional hay meadows rich in species such as Autumn Hawkbit *Leptodon autumnalis* or in fields and moorland areas with large clumps of seeding thistles (particularly those of Spear *Cirsium vulgare*, Marsh *C. palustre* and Creeping Thistles *C. arvense*). Protecting key sites, particularly through programmes such as the UK government's Entry and Higher Level Stewardship schemes, would provide a mosaic of suitable feeding areas for Twite over a large area. Furthermore, the removal of key feeding sites, particularly of upland hay meadows, is likely to have an adverse effect on Twite breeding in colonies over a wide area. Conservation action for Twite should therefore be considered at a landscape level.

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