Studies of West Palearctic birds

196. Common Starling *Sturnus vulgaris*

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The Common Starling *Sturnus vulgaris* is a member of a family of about 110 species whose distribution is entirely Old World, concentrated primarily in sub-Saharan Africa and Southeast Asia. In its family, the Common Starling is unusual in that it has moved away from these main centres of distribution in the Afrotropical and Indo-Malayan regions, and inhabits a huge geographical area in the Palearctic. This range extends from the Azores in the west to Lake Baikal in the east, and from Lapland in the north to Sind, Pakistan, in the south (Cramp & Perrins 1994). Northern and eastern populations are migratory, wintering to the south, southwest and west of their breeding areas, while some of the southern and western populations are resident. Dementiev & Gladkov (1957) provided a distribution map which showed, in addition to the range described above, an intriguing question mark in the east of the then Soviet Union. Since the 1970s, small numbers of Common Starlings have wintered in Hong Kong (Chalmers 1986) and Japan (Brazil 1990); the origin of these wintering birds in the far east is not known, but perhaps Dementiev & Gladkov's (1957) query over the existence of Common Starlings on the eastern seaboard of Russia has some foundation.

In addition to the geographical range outlined above, Common Starlings have proved to be eminently capable of establishing themselves in new environments following introduction by Man. They were successfully introduced to New Zealand by Acclimatisation Societies, whose aim was to provide new human immigrants with a taste of 'home' by attempting to establish wildlife common in England. Thomson (1922), however, claimed that some of the introductions were to control outbreaks of insects that occurred in the mid 1800s. Acclimatisation Societies were also responsible, along with private individuals,

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for introducing Common Starlings to Australia, some of the birds being taken there from New Zealand. According to Lever (1987), Common Starlings were taken from southern England to South Africa in 1897 by Cecil Rhodes and released in Groote Schuur, Rondebosch. In all of these countries the introductions have been successful, and in Australia and South Africa the birds are continuing to spread. In biological terms, perhaps the most successful introduction has been in North America. In the early 1890s, Eugene Schieffelin, an apparent eccentric who thought that America should have all the birds mentioned by Shakespeare, imported Common Starlings from England and released them into Central Park, New York. From this introduction, though apparently not from earlier or later attempts (Lever 1987), Common Starlings have within a century colonised North America. They now have a breeding range that extends from east-central Alaska through northern Manitoba to Newfoundland in the north, and to Baja California in Mexico, southern Texas and the Gulf coast to southern Florida in the south (AOU 1983), and are one of North America's most numerous birds. This colonisation of North America is all the more remarkable in that it has occurred in a continental environment which already possessed species with many apparently similar ecological requirements, notably various members of the Icteridae, such as the Red-winged Blackbird *Agelaius phoeniceus* and the Brown-headed Cowbird *Molothrus ater* (Feare 1984). The Common Starling's success as an exotic is not confined to temperate regions, for it has also become established on the tropical islands of Fiji (Watling 1982) and Jamaica, where numbers have increased rapidly over the last 25 years (Downer & Sutton 1990).

**Habitats and populations**

Common Starlings are adaptable in their choice of habitats, appearing equally at home in farmland, open woodland and suburban gardens. Large summer feeding flocks are found on moorland and coastal saltmarsh, and city centres provide roost sites for spectacular numbers.

Common Starlings have powerful legs which are used for walking, rather than hopping, and the head and its muscles permit the use of a specialised feeding technique. This 'prying' (Beecher 1978) involves inserting the closed bill into the surface of a grass sward and then opening it using powerful protractor muscles, which in Common and related starlings are larger than the adductor muscles which are used to close the mandibles. This technique is used to expose invertebrates and sometimes seeds which lie among the grass roots or surface soil, and is a technique that superbly adapts Common Starlings to exploit extensive grasslands. Starlings also pry when selecting food items of a particular size from an apparent superabundance, for example when taking fragments of barley from cattle feed, and when searching for food among seaweed on the shore and among stones on the filter beds of sewage-treatment plants. The birds' feeding is not restricted to prying, however, and Common Starlings commonly forage in trees, both to eat fruit and, especially in summer, to exploit abundances of defoliating caterpillars (Feare 1984). They occasionally take nectar (Feare 1993) and hawk flying insects, especially when winged ants emerge. The Common Starling's consumption of fruit, cattle food, pig food and poultry food, and of germinating cereals has brought the species into conflict with farmers in many parts of its
Plate 178. Common Starling *Sturnus vulgaris*, Worcestershire, December 1995 (Mike Wilkes). Although showing the white-tipped breast and belly feathers of winter plumage, the underlying iridescence is clearly visible.

Plate 179. Common Starling *Sturnus vulgaris*, Norfolk, March 1983 (Kevin Carlson). In autumn and winter, body feathers are edged buff or white; these become abraded later, leaving the glossy plumage typical of the breeding season.
Plate 180. Male Common Starling *Sturnus vulgaris* singing, with throat, belly and rump feathers fluffed, and tail directed downwards, Netherlands, March 1992 (René van Rossum)

Plate 181. Male Common Starling *Sturnus vulgaris* carrying leatherjacket (larva of cranefly, Tipulidae), Tiree, Strathclyde, May 1992 (Gordon Langbury). The pale feather tips have worn away, leaving brilliant glossy plumage. At this stage in the breeding season, the bill is yellow (with a steel-blue base in the case of males) and the legs and feet are pink.
range (Feare et al. 1992), although some farmers consider that the bird’s consumption of insect pests outweighs other problems (Feare 1984).

Although primarily adapted to feeding in grasslands, for which they show a marked preference in farmland (Whitehead et al. 1995), in the breeding season the birds’ distribution is restricted by their requirement for nest sites, for they are cavity nesters. Here again, however, they show great adaptability and, while holes in trees comprise the most usual nest sites, they also use holes in cliffs, banks, walls, buildings and other man-made structures. They also occasionally nest underground, and have even been recorded burrowing their own nest holes in sand dunes (Summers 1989a) and in softer soils in cliff faces (Stevenson 1866).

At all times of year Common Starlings roost communally at night. These roosts are smallest during the breeding season, when they contain only non-breeding birds and some breeding males, and largest in winter (Eastwood et al. 1962). At the latter season, roosting assemblages can be spectacular, as huge numbers, occasionally a million or more in Britain, gather in nearby trees and fields. These birds depart for the roost site in vast flocks, and then often manoeuvre in cloud-like swirls before descending into the roost. The largest roosts are found in rural areas, usually in small woods or reedbeds, but impressive numbers can also be seen roosting on bridges, piers and other man-made structures, and especially on buildings or in trees in city centres. City-centre roosts promote mixed feelings in humans, for, while some like the spectacle of large numbers of birds in otherwise fairly birdless places, others complain of the noise made by the birds and the huge quantities of droppings they deposit. The latter can render paved surfaces dangerously slippery and buildings unsightly, and cleaning operations can impose expensive burdens on local authorities and others (Feare 1985). In large rural roosts, the weight of birds on tree branches can break them and this, combined with the huge quantities of droppings, is claimed to kill trees in plantations selected by the birds for roosting (Feare 1984). Reedbeds are also flattened by roosting Common Starlings, and, when reeds were regarded as a valuable resource for roofing thatch, this damage was regarded as economically serious (Gurney 1921).

The history of Common Starlings in Britain has been one of change. The presence of outlying populations of distinct subspecies and even a distinct species (the Spotless Starling S. unicokr) suggests that S. vulgaris once had a geographical range in western Europe at least as large as it is today, but that this range contracted at some stage (Feare 1984). In the early eighteenth century, the Common Starling had disappeared from many parts of Britain, being absent from much of western England and Wales, western Ireland and mainland Scotland, and was rare in northern England (Holloway 1996). From about 1830, the population began to expand and to recolonise areas that had been vacated, and this expansion continued to the 1960s (Parslow 1968). The reasons for these changes are unclear. Since 1962, we have had the advantage of the British Trust for Ornithology’s Common Birds Census (CBC), which has given us a better, although not complete, picture of events up to the present day. High indices of the population in the early 1960s fell sharply in the latter part of that decade and recovered only slightly in the 1970s. Through the 1980s the indices for both farmland and woodland fell steadily, and by 1988 the farmland population had decreased by 50%, and that of woodland by 67%, from the levels of the mid 1960s (Marchant et al. 1990). These declines have continued in the
1990s, and by 1994 the woodland index had fallen to 25% of its 1980 value (Marchant & Wilson 1995). These figures may present a somewhat biased picture, since CBC sites tend to be concentrated in the south and east of England, where agricultural intensification has been particularly great. In addition, urban and suburban areas are not covered by the CBC, but, in suburban Surrey, a nestbox colony in which over 30 boxes were occupied in the 1970s declined to an occupancy of only seven boxes in 1994 and 1995, a 75% reduction (Feare, unpublished data).

That these declines are real and significant is supported by similar, and in some cases larger, declines in continental Europe. Colony reductions, and even extinctions, were first reported from Finland in the late 1960s (Ojanen et al. 1978), and subsequently from many other parts of northern Europe. This has had implications farther south, for the wintering populations of western Europe have also shown marked reductions, although precise data on their extent are lacking (Feare et al. 1992). The outcome of this is that agricultural damage, especially through the birds' consumption of cattle food, for which the birds were notorious in winters of the 1970s, has now diminished. The factors underlying these population changes are unclear, and climate, agrochemicals and changes in land use may all be involved. The last may be an important influence in the recent decline in Britain, where loss of grassland to cereal production and the switch from spring to autumn cultivation are likely to have reduced the Common Starling's winter food supply (Feare 1994). The species' decline seems to have spread beyond western Europe, however, for the numbers that winter in Israel have also fallen from an estimated 15 million in 1970 to one million in the early 1990s (Yom-Tov in litt.).

While northern Europe witnesses declines in the populations of one of its most serious agricultural pests, southern Europe is seeing the reverse, with potentially interesting consequences. In southwest France and northeast Spain, the ranges of starlings, both Common and Spotless, are expanding, and both species have crossed the Pyrénées (Peris et al. 1987; Cambrony 1990), resulting in the formation of some mixed-species pairs (Motis 1992).

Complexities of song

Common Starlings are not renowned as melodic songsters, but their capacity to mimic the calls of other species of birds, and even other sounds, is well known. Mimicry, however, forms only a small part of the song (Hindmarsh 1984), and what the song lacks in musical quality it compensates for in complexity.

Song is heard at its fullest as males seek mates before the onset of egg-laying and, after pairing, during the female's fertile period (Eens et al. 1994). The male delivers more than 95% of his song in bouts (more-or-less uninterrupted periods of singing) which can be long, sometimes lasting for more than a minute. Song bouts consist of a rapid succession of a wide variety of song types, and the number of song types used by an individual male comprises his repertoire. Recent studies of the organisation and variability of these song types, and of differences in repertoire size between individuals, have provided insights into the functions of song in Common Starlings.

Song types fall into four categories and these are delivered in sequence (Adret-Hausberger & Jenkins 1988; Eens et al. 1991a). A song bout usually begins with
relatively simple pure-tone 'whistles'; these are followed by complex 'variable' song types, which are in turn succeeded by 'rattles', and the bout finishes with 'high-frequency' song types. When individual Starlings omit one of the categories from a song bout, the bout always continues with the next category in the succession. In a study of the songs of 25 male Common Starlings in Belgium, Eens et al. (1991a) found that the majority of song bouts began with one or several 'whistles', but that individual males varied in their propensity to begin their song bouts with these song types. Different males had between two and 11 whistles in their repertoires.

'Variable' song types were much quieter than the 'whistles', but were much more complex and included the mimicked calls of other species. Different males had repertoires of ten to 35 song types in this category, and each of the song types was repeated before moving on to the next. 'Rattle' song types, involving a rapid succession of clicks, were also repeated, and males had between two and 14 of these song types in their repertoires. The loudest song types delivered in a song bout fall into the last category, the 'high-frequency' types, and individual males had between none and six of these in their repertoires, which again were repeated before moving on to the next. The 25 males revealed large differences in their repertoire sizes, varying from 21 to 67 song types between individuals, and those with the larger repertoires tended to have longer song bouts.

Some of the variability in both song-bout length and repertoire size has been found to be associated with the age of the males. Eens et al. (1992a) demonstrated that older Starlings had larger repertoires and longer song bouts than one-year-old birds, and Böhner et al. (1990) and Mountjoy & Lemon (1995) have shown that Common Starlings are able to learn new song elements as they become older. The latter authors found that between years some song types were dropped from the repertoires and others were modified, but that even four-year-old Starlings were capable of learning new song types and incorporating them into their repertoires. There is now evidence that some of the variability in song-bout length and repertoire size has a structural basis, for there are correlations between these song parameters and the size of certain song nuclei in the Starling's brain (Bernard et al. in press; Eens in press).

Mimicked sounds may be incorporated into the song bouts, in the 'variable' song (Eens et al. 1991a; also called the 'warbling' song by Adret-Hausberger & Jenkins 1988) and in the 'whistle' song types (Hausberger et al. 1991), and also in the small proportion (< 5%) of song that is delivered independently of song bouts (Eens et al. 1991a). The sounds that are mimicked are not necessarily those that are likely to be encountered most frequently in the birds' surroundings and there is clearly selection of sounds from those available to be copied (Hausberger et al. 1991). Among the whistled song types, selection of models to mimic seems to be related to the structure of the model's call rather than the particular species concerned; simpler calls, more like the Starling's 'whistles', are more likely to be copied than are other calls. The outcome of this is that the range of calls of other species incorporated into the whistled song types is restricted and bears similarities over large geographical areas (Hausberger et al. 1991). Mimicked sounds that are incorporated into the 'variable' song types are quieter but more complex, and structurally more similar to variable song types than to other song types found in
bouts, and include trills and sounds made up of several notes, often involving fragments of other species’ songs. These mimicked sounds bear a closer resemblance to the Starlings’ immediate environment (Hausberger et al. 1991), although Eens et al. (1992b) established that some mimicked song types were learned from other Starlings, rather than from the other species themselves. The complexity of song of the Common Starling, to which mimicry contributes, permits this song to contain both species-specific song types and song types that are unique to individual males.

Cuthill & Hindmarsh (1985) demonstrated that after pairing the amount of song delivered by a male decreases, indicating the role of song in mate acquisition. This was further demonstrated by Eens (in press), who found that unpaired male Starlings increased their song output in the presence of prospecting females, and often flew into their nest and sang there, in an apparent attempt to entice the female towards the nest hole. Eens et al. (1992a) found that, while the repertoires of ‘whistled’ and ‘high-frequency’ song types showed little difference between yearling and older males, the latter’s repertoires of ‘variable’ and ‘rattle’ song types were approximately twice as large as those of the younger birds. These authors (Eens et al. 1991b) further found that males with longer song bouts and with larger repertoires attracted mates earlier, attracted more mates, and had higher breeding success than males with shorter bouts and smaller repertoires. Females thus appear to select preferentially those males with more complex songs, possibly because song provides an index of male experience or survivorship. In addition, Mountjoy & Lemon (1996) found that males with large song repertoires were in better body condition, allowing females to select mates which, on the basis of their song, are likely to be of higher quality. Mountjoy & Lemon (1991) also demonstrated a role of song in male-male interactions, showing that recorded playback of more complex song was more effective at deterring males from entering nestboxes than were simpler songs. This suggests that male Common Starlings might be able to assess the competitive ability of other males on the size of their song repertoires, and that song may therefore play a further role in territory defence.

Common Starlings also sing outside the breeding season; in fact, they sing for most of the year, ceasing only for a brief period during the moult (Feare 1984). Adret-Hausberger (1982) reported that different whistle types were sung in different flock sizes, and that a further whistle type was characteristic of song in roosts. Song outside the breeding season has been little studied, however, and its function requires further investigation (Eens in press). Female Common Starlings also sing and, according to Hausberger et al. (1995), they do so more in autumn and winter than in the breeding season. In the breeding season it was found that females sang when competition between females was intense and that song was directed at other females, rather than at males (Sandell & Smith in press; Eens & Pinxten 1996). Female song is not confined to aggressive situations, however, as Hausberger & Black (1991) observed two females of a polygynous male (see below) indulging in bouts of song-matching with no sign of antagonism. The function of female song outside the breeding season is, as with male song at this time of year, not understood, although both sexes sing during the occupation of roost perches and here song appears to have a role in roost-site acquisition and defence (personal observations).
Complexities of breeding

Common Starlings nest in holes in trees, buildings and other structures. The dispersion of nesting Starlings is determined by the availability of suitable holes, and nests may therefore be several metres or tens of metres apart. Despite the sometimes large inter-nest distances that are imposed upon the birds, Common Starlings behave as colonial breeders and the onset of laying each year is highly synchronised among nests. Although mainly under photoperiodic control, the time of breeding each spring is influenced by other factors, including temperature and food availability (Källander & Karlsson 1993; Meijer & Langer 1995). The fine tuning that facilitates the high degree of synchrony seen in Starling colonies probably results, however, from the birds’ social behaviour within the colony, although this aspect of Starling behaviour has not been studied.

While at one time considered to be monogamous (Lack 1968), recent studies have shown that Common Starlings can sometimes be polygynous, that they frequently exchange mates, that some females lay their eggs in other Starlings’ nests, that some females copulate with males other than their mates, and that occasionally two females may nest communally. These departures from strict monogamy are all facilitated by the synchrony of behaviour that accompanies the onset of each breeding season.

As described above, male song serves as a mate attractant. Paired males sing from song posts near their nests and this stimulates their mates to fly towards them and solicit copulation (Eens & Pinxten 1990). These authors also observed paired males attempt to stimulate the female mates of neighbouring males to copulate. In these instances, the paired males behaved differently, flying towards the non-mate

Plate 182. Male Common Starling *Sturnus vulgaris* singing and wing-waving, Western Isles, April 1989 (G. P. Catley). The wings are half extended and rotated about the shoulder. This behaviour is used primarily in spring, by a male trying to attract a female flying nearby.
females and singing close to them. On one occasion, a male was seen to copulate successfully with his neighbour's mate. The success of some extra-pair copulations has been confirmed genetically by Hoffenberg et al. (1988), Pinxten et al. (1993a) and Smith & von Schantz (1993). Cuckoldry represents a means whereby males may increase their output of offspring and mated males endeavour to protect their females, and thus their own paternity, by closely guarding their mates during their fertile period (Pinxten et al. 1987). Eens & Pinxten (1990) thought that polygynous males might be more susceptible to cuckoldry than monogamous males, but the studies of Pinxten et al. (1993a) and Smith & von Schantz (1993) provided no evidence for this.

In many colonies, Common Starlings lay two clutches each year; in other words, a female who has successfully reared one brood to independence returns to the colony and lays another clutch in the same year. The proportion of females that attempt to rear two broods varies both between years and geographically, with birds in the south and west of their range in Eurasia rearing two broods more often than their comrades in the north and east (Feare 1984). Between the two clutches, however, the females frequently exchange mates and nest sites (Feare & Burnham 1978), so that the progeny of a particular female during a year may be fathered by more than one male.

In colonies where two broods are reared, there are two peaks of laying: the first, highly synchronous peak at the beginning of the breeding season; and a second, smaller and less synchronous group of clutches initiated about 45 days later, although some of the clutches laid at this time are not second clutches, but first clutches of females that begin laying late. Between these two peaks, other clutches, usually termed 'intermediate' clutches, are laid. These include first clutches of females that do not lay until after the main peak of laying, replacement clutches of females that lose their first clutches, and clutches of females that are mated to males who already have a first mate incubating a first clutch (Pinxten et al. 1990). Some males, especially older ones, may have two females during the laying peak corresponding to first clutches. Such polygyny is now known to be widespread in Starlings and, at a colony in Belgium, Pinxten et al. (1989a) found that, over a four-year study, 20-60% of males were polygynous each year. While most polygynous males have two mates, exceptionally up to five females may be mated to one male (Merkel 1978; Pinxten et al. 1989b). Males which are polygynous produce more fledglings than do monogamous males (Pinxten et al. 1989a), but being the mate of a polygynous male seems to be disadvantageous for females, since they produce fewer young than do monogamous females (Pinxten & Eens 1990). This may result from a difference in the behaviour of monogamous and polygynous males, for polygynous males devote less time to the care of their eggs and young than do monogamous males (Pinxten et al. 1993b). The primary female (the first female) of a polygynous male can compensate for the reduced contribution of her partner by increasing her own contribution of food to the nestlings, but secondary females appear unable to do this and they fledge fewer young than do primary and monogamous females (Pinxten & Eens 1994). Some later-arriving females have little opportunity to be monogamous as, by the time of their arrival, all males already have mates, but there is clearly a conflict of interests between the sexes early in the breeding season. Males appear to benefit by seeking more than one mate, while females are disadvantaged if they mate with males who are, or are going to be, polygynous.
Plate 183. Male Common Starling *Sturnus vulgaris* arriving at nest with several food items in bill, Co. Cork, May 1987 (Richard T. Mills). Note pointed wings and short, square tail, which contribute to the species' characteristic flight silhouette.

Females attempt to defend their interests by discouraging their males from seeking other mates; females increase their attempts to solicit copulation from their mates when the latter encounter new females, and also act aggressively to new females (Eens & Pinxten 1995a, 1996), and primary females may even desert their clutches/broods, possibly as an attempt to force the male to care for the brood (Eens & Pinxten 1995b). Despite their lower productivity, however, some earlier-arriving females appear to choose to be polygynous, for reasons that are unclear (Pinxten & Eens 1990).

Intraspecific nest parasitism, where some female Common Starlings lay eggs in other Starlings' nests, was first recorded by Yom-Tov et al. (1974), but this behaviour has also proved to be common and widespread. In colonies that have been adequately studied, up to 37% of first clutches have been found to contain an egg that had not been laid by the female who owned the nest (Karlsson 1983; Evans 1988; Lombardo et al. 1989; Pinxten et al. 1991a; Romagnano et al. 1990). These authors identified parasite eggs by several methods: the appearance of two eggs within a 24-hour period, the presence of an egg that differs in colour, shape and size from other eggs in the clutch, and the presence of a chick whose blood biochemistry indicates that it is not related to the parents of the remainder of the brood. All of these techniques tend to underestimate the incidence of parasitism (Pinxten et al. 1991b), so that the recorded incidences of nest parasitism are minimum figures. (DNA fingerprinting will allow more accurate determination of the incidence of this behaviour, but studies have so far been limited to colonies where brood parasitism appears uncommon: Pinxten et al. 1993a; Smith & von Schantz 1993.) The frequency of this behaviour suggests that it is a strategy
adopted by some females, but an interpretation of the function of the behaviour requires identification of the females who parasitise, and this has proved difficult. Nevertheless, there is now sufficient information to show that females may become parasites for a number of reasons.

Evans (1988) found that the incidence of parasitism was greater when large numbers of females deserted their first clutches. Most of these desertions resulted from disturbance caused by catching nesting adults, and Feare (1991) showed that females whose laying in their own nest was interrupted continued to lay their remaining first-clutch eggs in other Starlings’ nests. Parasitism thus enabled such females to give these remaining first-clutch eggs the chance of survival in other nests, and allowed these females to rear a replacement clutch of their own; this was more beneficial, in terms of chick production within the year, than continuing to lay in their own nests and rearing an unusually small first clutch (Feare 1991).

Evans (1988) also suggested that nest parasitism might be related to competition for nest sites, but the support for this is equivocal. Evans (1988) and Karlsson (1983) found higher levels of parasitism when a greater proportion of available nests was occupied, but Pinxten et al. (1991a) and Romagnano et al. (1990) recorded high levels of nest parasitism when nest-site occupancy was low, and in my own study colony parasitism still occurs each year despite a 75% fall in the breeding population but no reduction in nest-site availability.

Evans (1988) and Romagnano et al. (1990) suggested that some parasitic females might be unmated and were generally young birds which had been fertilised by an already paired male, but which did not possess nests of their own. Pinxten et al. (1991a) obtained circumstantial evidence that some parasitic females may fall into this category, but this possibility is difficult to test experimentally.

A further suggestion is that some female Common Starlings operate a mixed strategy, rearing a clutch of their own but also depositing an egg in another Starling’s nest, thereby spreading their potential offspring and insuring against total failure of their own clutch (Møller 1987; Brown & Brown 1989). Evans (1988) recorded some females laying an egg in another Starling’s nest while rearing a clutch of their own, and I have also recorded this in my study colony. It is, however, difficult to know whether this really represents a mixed strategy on the part of these females, or whether these observations reflect an extension of the parasitism that results from disturbance; females who are disturbed when ready to lay in their own nests may opt to lay this egg in another nest, rather than wait for the disturbance to pass and return to their own nest.

Intraspecific nest parasitism among Common Starlings is accompanied by behaviours that help to ensure the success of the parasitic female’s egg, and that help potential hosts to guard themselves against parasitism. Feare et al. (1982) found that, while most Common Starlings laid their eggs during a restricted period in the morning, some eggs laid by parasitic females appeared in nests in the afternoon, suggesting that parasitic females may avoid the time when hosts are most likely to be in the vicinity of their nest. Pinxten et al. (1991b) were able to watch parasitic females and discovered that they laid their eggs remarkably quickly, which may also help to avoid the attention of potential hosts. There is also evidence that at least some parasitic females remove a host egg when they lay their parasite egg. Lombardo et al. (1989) reported that eggs
were removed more often from parasitised than from unparasitised nests, and found a statistical relationship between the deposition of parasite eggs and the removal of host eggs. Evans (1988), Pinxten et al. (1991a) and Feare (1991) also recorded egg removal from nests in which parasite eggs were laid, and Pinxten et al. (1991a) directly observed parasitic females removing host eggs at the time they laid their own. Egg removal, however, is also practised by hosts as a defence against parasitism, although hosts are unable to differentiate between their own and parasite eggs and remove the latter only if they appear in nests before the host has initiated its own clutch (Stouffer et al. 1987); both male and female remove such eggs, the female being more assiduous in the task. Power et al. (1989) suggested that a further defence against parasitism involved female Starlings laying fewer eggs than they could in practice raise to fledging; this provided an insurance against the eventuality that an extra parasite egg might be laid in their nest, but this hypothesis has been disputed by Rothstein (1990).

Communal breeding has been recorded twice for Common Starlings. Both instances involved two females laying in one nest, with both females and a single male assisting with incubation and feeding the young (Stouffer et al. 1988; Pinxten et al. 1994). In the latter instance, the paternity of the male in the clutches of both females was confirmed by DNA fingerprinting. This communal breeding by Common Starlings is probably rare, as unusually large clutches of eggs were involved, and it differs from the co-operative breeding by some other starling species (Craig 1987) in which a breeding pair is assisted in the raising of a brood by other non-reproductive conspecifics.

Plate 184. Juvenile Common Starlings *Sturnus vulgaris* showing threat posture, with upright stance, raised crown feathers and fluffed belly feathers, but plumage otherwise sleeked, West Glamorgan, June 1986 (Harold E. Grenfell)
Roosting

The gathering of huge numbers of Common Starlings into night roosts is one of the most spectacular sights in ornithology. Most night roosts, and especially the larger winter roosts, are in rural areas, but city-dwellers can get a taste of the birds' behaviour as many city centres now host roosts, sometimes containing many thousands of Starlings which spend the night on trees or on ledges of buildings. The behaviour of Starlings which roosted in central London was studied by Stanley Cramp and colleagues from the London Natural History Society in the late 1940s and early 1950s (Cramp et al. 1964). These authors found that the tens of thousands of birds involved were largely resident British Starlings that fed in the suburbs. The birds' assembly in the afternoon and their presence in the city centre, especially in Trafalgar Square, at night brought them to the attention of the public and the media. On 12th August 1947, assembling Starlings landed on the minute hand of Big Ben and the weight of birds involved was sufficient to stop the clock. This and other problems led to questions being raised in Parliament and, unique as an accolade to a British bird, the Starling became the subject of an episode of The Goon Show!

Common Starlings roost communally throughout the year, but during the breeding season roosts are small and are used by non-breeders and some breeding males (Cramp et al. 1964; Feare 1984). During the winter, when the largest roosts are observed, Clergeau (1993) found that large roosts in France were composed mainly of migrants; resident birds remained close to their nest sites throughout the winter and roosted nearby in small assemblages of five to 100 birds.

During the day, Common Starlings feed away from the roost and in winter have been recorded commuting up to 80 km each day to feed (Hamilton & Gilbert 1969), although most feed well within this range. Starlings can be remarkably faithful to a particular feeding area over long periods (Feare 1980;}

Plates 185 & 186. Pre-roost mass aerial displays by Common Starlings *Sturnus vulgaris*, Lincolnshire, January 1979 (C. J. Feare)
Morrison & Caccamise (1985), although such fidelity may be a characteristic of older birds, first-winters having been observed to sample a wider range of feeding sites within a winter (Summers & Cross 1987). Morrison & Caccamise (1985) found further that Starlings remained faithful to their feeding areas, which these authors termed 'daily activity centres', even though the roosts to which the birds returned each night switched position periodically. During their return to a roost in the late afternoon, Starlings gather in large flocks, usually within 2 km of the roost site. In these 'pre-roost assemblies' the birds may sing, bathe and preen, but the main activity is to feed intensively, and the sites at which pre-roost assemblies form must thus represent good feeding sites. Summers (1989b) found that this was indeed the case, and pre-roost assembly sites were often traditional sites, used each evening, where food was superabundant, for example pig farms and cattle farms where food was put out freely for the stock.

Caccamise & Morrison (1986) considered that these sites, where Starlings could obtain a large amount of food just before entry into the roost, were the determinants of the locality of the night roost and that depletion of food at these assembly areas led the birds to change roost sites, while still remaining faithful to their daily activity centres. Fidelity to daytime feeding areas allows Starlings to learn where good-quality food can be most profitably obtained (Peach & Fowler 1989), for Starlings can be highly selective in the food that they take (Tinbergen 1981), and an adequate supply of invertebrates is essential for survival, even in winter (Feare & McGinnity 1986). At their feeding sites, Starlings also require daytime roost sites and drinking-and-bathing areas, and familiarity with the environs of the daily activity centre presumably enables the birds to learn where these activities can be undertaken with maximum safety from predators and shelter from adverse meteorological conditions.

The most spectacular part of roosting behaviour is seen after the Starlings leave the pre-roost assemblies and just before they descend into the roost site where
they will spend the night. At this time, huge flocks often fly over the roost site in swirling smoke-like or cloud-like masses, the birds in each large group appearing to act as a co-ordinated unit so that all members of a flock seem to change direction instantaneously. Flocks eventually approach the roost site and fly low over it but at the last minute fly up again to rejoin the main groups above. This gives the appearance of reluctance to enter the roost until sufficiently large numbers are prepared to do so at the same time. An occurrence that a group of colleagues and I witnessed at a winter roost provided anecdotal support for this idea. In this case, a flock of about 20 Starlings broke from the main groups and flew into the trees; as they entered the tree tops, four Eurasian Sparrowhawks *Accipiter nisus*, which had clearly been waiting in the wood, lifted from the trees and each took a Starling. Thus, 20% of this first flock that attempted to enter the roost was taken by predators. Large traditional Starling roosts are regularly frequented by a range of avian predators (Feare 1984) and the aerial displays performed by birds prior to entry into the roost may serve as a protection from predation.

Within the roost, the distribution of birds is not random. They segregate into age groups and sex groups, such that adult males tend to occupy central positions and younger birds, especially females, distribute themselves around the periphery (Summers *et al.* 1987). As birds settle into the roost each evening there is considerable jostling for position, accompanied by much singing, and dominant birds generally secure the preferred sites through competition. Starlings prefer more central and higher positions (Feare *et al.* 1995), and Yom-Tov (1979) demonstrated a disadvantage of lower positions where the plumage of lower birds became contaminated with droppings from birds above, reducing the waterproofing qualities of the feathers. The position secured by Starlings within a roost may also influence their susceptibility to adverse microclimatic factors, especially wind, and predation (Feare 1984). Normally, roosting Common Starlings maintain a distance of 15-20 cm between individuals, but during extreme cold they may huddle together (Peach *et al.* 1987).

Morning departure from a roost also has its characteristic organisation, with birds leaving in co-ordinated exoduses, rather than as a continuous stream of birds. Exoduses are on average about three minutes apart, and observations using radar indicate that birds from each exodus travel to the limit of the catchment of roosts (Eastwood *et al.* 1962), although observations from the ground show that many birds from each exodus stop at feeding sites closer to the roost. Summers & Feare (1995) found that, during departure, adult Starlings tended to leave in earlier exoduses and young birds left in later ones, but there was no difference in the distance that birds of different age/sex travelled to their daily feeding areas. There were, however, differences in the social structure of flocks that fed at different feeding sites, and Summers & Feare (1995) suggested that this was related to differences in the quality of food available at the different sites. These authors concluded that these departure patterns enabled dominant birds, mainly adult males, to secure the better-quality feeding sites, while later-departing subordinate and younger birds could judge the likely competition they might face as they overflew these sites; they could then decide whether to attempt to feed there or to fly on to sites that were inferior but where they could feed in the absence of intense competition from more dominant individuals. The reason for the birds' departure in a series of well-co-ordinated exoduses remains unknown.
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