# AN ECOLOGICAL STUDY OF THE INSECTS AND MITES IN THE NESTS OF CERTAIN BIRDS IN BRITAIN.

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(Plates XIV, XV and XVI.)

Contents.



The work upon which this paper is based was carried out in England during the autumn and winter of 1950, and the early spring of 1951. Previously, during the first three months of 1950, some exploratory work was done, and the results have already been published (Woodroffe & Southgate, 1951a). In addition, two short notes have been published which deal with specific points (Woodroffe, 1950; Woodroffe & Southgate, 1951b). One of the most important items in the literature on this subject is the paper by Linsley (1944) in which he gathers together many scattered records, contributes a number of his own, and summarises the position at that date. Most of the available records of insects occurring in birds' nests can be traced through the references given by that author and by Hinton (1945). However, one paper seems to have escaped the notice of both these workers, and the writer is indebted to Mr. G. B. Thompson for drawing his attention to it. This is the work of Nordberg (1936), and it is the most important contribution that has so far been made towards our knowledge of nest fauna. Nordberg's paper will be summarised and his results examined in the last section of this paper.

A recent publication by Weidner (1952) deals with the insect ecology of the city of Hamburg. This contains many references to nest insects and includes a useful bibliography. Weidner, also, has overlooked Nordberg's work.

The general background to the present work has been given in the earlier paper, and so will be mentioned only briefly here. The survey was conducted with the following three points as its chief aims:—

1. The collection of sufficient information on nest fauna to enable an assessment to be made of the importance of birds' nests as reservoirs of domestic and storage pests in Britain.

2. The study of the habits and behaviour of pest species in the nest habitat in order to supplement or confirm information gained from laboratory life-history studies.

3. The study of the nest as a microhabitat.

The facts presented in this paper add to existing knowledge on all three points.

The most important conclusion reached during the preliminary work was that the humidity conditions within a nest are of primary importance in determining the composition of the scavenging fauna. Nests may be classified as "wet" or "dry" according to whether they are exposed to, or protected from, rain or drainage water. The effect of humidity conditions upon the composition of the insect fauna will be discussed in detail later. It is only necessary here to explain that, having established the difference between the two types of nest, this survey covered only "dry" nests and, unless a statement to the contrary is made, it is this type of nest which is referred to throughout the paper.

## Methods.

The method of examining material has remained substantially the same as that described previously (Woodroffe & Southgate, 1951a). It consisted of sieving the disintegrated nest material and warming the various fractions on a tray over a hot-plate. The use of such methods as the Berlese funnel were found to be impracticable for several reasons. The quantity of material to be examined was often very large and the presence of material varying from large twigs to extremely fine dust necessitated a considerable amount of preliminary separation; many insects were present in an inactive stage, and some, such as the case-bearing Tineid larvae, experienced considerable difficulty in moving rapidly in a definite direction through the type of material that contained them; also, it was found that some insects—*e.g.*, Dermestid larvae—could be driven out only by heat treatment which would be rapidly lethal to other insects, such as lepidopterous larvae. In any case, it was often necessary to rear the adults in order to identify some of the species with certainty, and this precluded the use of any automatic method of separation which involved killing the insects.

In the absence of a suitable method of automatic collection of high efficiency, it was not possible to obtain precise quantitative information concerning the degree of infestation of each nest. Such figures would, in any case, be misleading, because even if nests are examined at the same time, the insect populations need not necessarily be in corresponding stages of development. Very large numbers of small larvae of a particular species could represent the same degree of infestation as much smaller numbers of full-grown larvae of that species if mortality in the early larval stages was normally high. Consequently, it was found more satisfactory to use a standard method of examination of nest material and to form a general opinion of the abundance of each species during the process of examination and collection. As the examination of each nest was completed, these estimates were recorded on a standard form by means of arbitrary symbols. Details of position and composition, and also subsequent identifications, were recorded on the same form. In one instance, a complete count was made of all the insects from a house-sparrows' nest in order to obtain some idea of the numerical value of the arbitrary estimates. Table I gives approximate values of

TABLE I.

Approximate numerical values of arbitrary estimates of abundance of several species of insects in a single nest.

| Arbitrary estimate of abundance | Abbreviation used in records | Approximate numbers per nest | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | *Hofmannophila pseudospretella* | *Tinea columbariella* | *Anthrenus verbasci* | *Attagenus pellio* | *Tenebrio molitor* | *Ptinus tectus* | Other *Ptinids* | *Lepisma saccharina* | *Scenopinus fenestralis* | *Lyctococris campestris* |
| Very large numbers | VLN | 500–1000 | 1000–3000 | 100–200 | 100–500 | 200–500 | 200–500 | 50–150 | 100–500 | 50–100 | 100–200 |
| Large numbers | LN | 100–500 | 500–1000 | 50–100 | 50–100 | 100–200 | 100–200 | 30–50 | 50–100 | 30–50 | 50–100 |
| Moderate numbers | MN | 50–100 | 100–500 | 20–50 | 20–50 | 50–100 | 50–100 | 20–30 | 20–50 | 20–30 | 20–50 |
| Small numbers | SN | 20–50 | 50–100 | 10–20 | 10–20 | 20–50 | 20–50 | 10–20 | 10–20 | 10–20 | 10–20 |
| Very small numbers | VSN | <20 | <50 | <10 | <10 | <20 | <20 | <10 | <10 | <10 | <10 |

these estimates for some of the more important insect species, all stages other than eggs being included. For some species (*Hofmannophila*, *Tenebrio*, *Ptinus tectus* Boield., *Lepisma*, *Lyctocoris*), the highest estimates were reached only in pigeons' nests, where it was often impossible to define exactly the limits of a single nest. The highest estimates for *Tinea columbariella* (Wocke) and *Anthrenus verbasci* (L.) usually occurred in house-sparrow nests.

## Faunal Lists.

Throughout the faunal lists, the species have been dealt with in one of three ways:—

1. Where a species is extremely abundant and widespread in nests, individual records would involve listing the localities of most of the hundreds of nests examined; consequently, only a general statement of the status of the species has been made, and only records of some special interest or significance have been detailed individually. The frequency of occurrence and abundance of most of such species are illustrated in fig. 1.

2. Certain groups of closely related species (*e.g.*, the Cryptophagid and Lathridiid beetles) have little importance as nest inhabitants or warehouse pests; such groups have been dealt with as units and detailed records for individual species have not been given.

3. Otherwise, where an insect is uncommon, its habitat unusual, or its distribution likely to be of interest to workers in the group, details of bird species, position of nest, locality, date and abundance * have been given for each record.

## The Insect Fauna.

### (a) Ectoparasites of Birds.

From the point of view of this survey, the bird parasites have little importance except as possible prey of predatory species. However, a number of records, particularly of the Cimicid bug, *Oeciacus hirundinis* (Jen.), and the Hippoboscid, *Stenepteryx hirundinis* (L.), have accumulated, and these may be of interest to those concerned with parasites. Detailed records of most parasitic species have been sent to Mr. G. B. Thompson for inclusion in his forthcoming publications. Consequently, only a simple list of species is presented here.

### Hemiptera.

Cimicidae.—*Oeciacus hirundinis* (Jen.).

### Diptera.

Calliphoridae.

*Protocalliphora azurea* (Fall.). This species was found to be very widespread in the nests of many species of birds. It appeared to thrive particularly in those of swallows. The puparia were frequently heavily parasitised by the Pteromalid, *Mormoniella vitripennis* (Walk.).

Hippoboscidae.

*Ornithomyia fringillina* Curt., *Ornithomyia avicularia* (L.), *Stenepteryx hirundinis* (L.), and *Crataerina pallida* (Latr.). Two puparia of *C. pallida* were parasitised by *Dibrachys* sp. (Hym. Pteromalidae). It has been possible to discover only very few other records of a successful attack by Hymenopterous parasites upon puparia of the Hippoboscidae, and none by *Dibrachys*.

* A key to the abbreviations used for the estimates of abundance is included in Table I.

**Siphonaptera.**

*Ceratophyllus hirundinis* (Curt.), *C. farreni* Roths., *C. columbae* Gerv., *C. gallinae* (Schr.), *C. fringillae* Walk. and *Dasypsyllus gallinulae* (Dale).

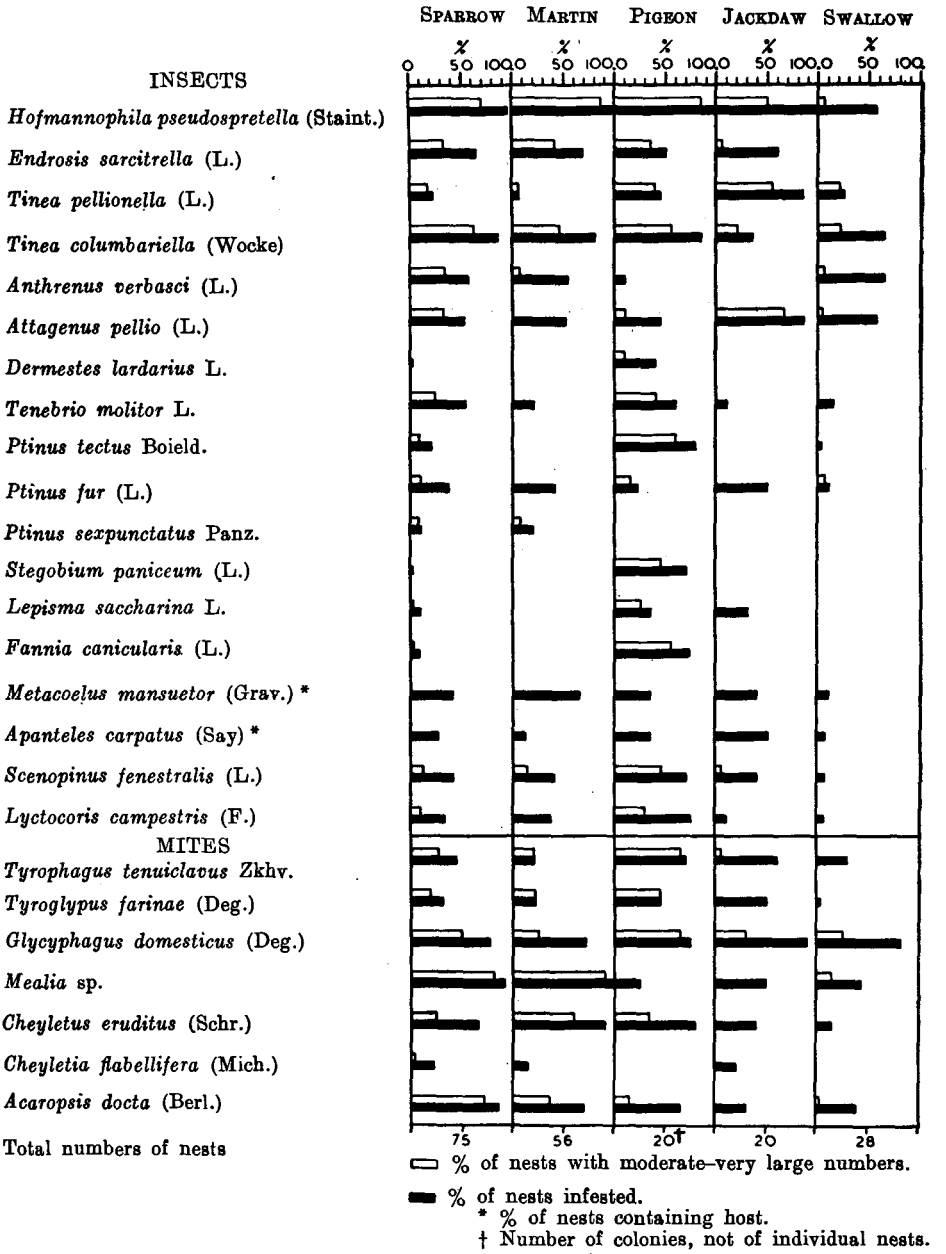


Fig. 1.—Frequency and abundance of some nidicoles in the nests of five bird species.

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## (b) Scavengers.

### Thysanura.

LEPISMATIDAE.

*Lepisma saccharina* L. The common silverfish occurred only occasionally in birds' nests in general, but sometimes very large numbers occurred in pigeon's nests. It is surprising to find this supposed starch feeder thriving in solid pigeon guano.

### Lepidoptera.

PHYCITIDAE.

*Ephestia elutella* (Hb.). A few larvae were occasionally found in sparrows' nests into which they had probably wandered from some other source. This is a major pest of grain, but there is no evidence that it can breed in nests in Britain.

*Records.* Sparrow, eaves of Parrot House, Regent's Park, London, 29 Sep. 50, VSN; sparrow, eaves of stables, farm at Wickham Bishops, Essex, 29 Nov. 50, VSN.

PYRALIDIDAE.

*Pyralis farinalis* (L.). *P. farinalis* is a minor pest of stored grain in Britain. It has been found only in pigeons' nests, but sometimes in some numbers.

*Records.* Pigeon (many nests), belfry, Chelmsford Police Station, Essex, 29 Nov. 50, MN; pigeon (many nests), bombed storage shed, Bristol, 18 Apr. 51, SN.

OECOPHORIDAE.

*Hofmannophila pseudospretella* (Staint.). The Brown House Moth is one of the commonest indoor moths in Britain. It has some importance as a general pest, attacking a wide variety of materials when the humidity is sufficiently high (Woodroffe, 1951), and may act as a grain pest or as a clothes moth. It is probably the commonest species found in nests, being absent only from some very dry swallows' nests, and is often present in very large numbers.

*Endrosis sarcitrella* (L.). This species, the White-shouldered House Moth, is very similar in importance to the last. It is often reported damaging stored beans and peas. It is generally less widespread and abundant in nests than *H. pseudospretella*, but may become dominant in nests such as those of titmice, which contain an abundance of green moss.

TINEIDAE.

*Monopis rusticella* (Clerck). This species is never an important pest, but is commonly found associated with stored products. It may be described as an intermediate species, occurring in both " wet " and " dry " nests, and was found principally in pigeons' nests.

*Monopis weaverella* (Scott). Ford (1949) summarises our knowledge of this species in five words—" In woods and on heaths." It was reared twice from pigeons' nests, both from the centres of large towns, and once from a jackdaws' nest in the country.

*Records.* Pigeon (many nests), turret, roof of hotel, Russell Sq., London, 25 Jan. 51, SN; pigeon (many nests), bombed storage shed, Bristol, 18 Apr. 51, VSN; jackdaw (several nests), hollow tree in meadow land, East Bergholt, Suffolk, 5 Oct. 50, VSN.

*Monopis crocicapitella* (Clemens). This species is sometimes associated with stored products of animal origin, and occasionally occurs in houses. Although seldom found in large numbers, it has, on one occasion, caused a major infestation (Woodroffe & Southgate, 1952). The larvae are case-bearers, and were found several times in some numbers in pigeons' nests.

*Records.* Pigeon (many nests), Railway Docks, Brentford, Middx., various situations, 15 Nov. 50, SN; pigeon (many nests), bombed storage shed, Bristol, 18 Apr. 51, MN.

*Tineola bisselliella* (Hummel). The Common Clothes Moth cannot be considered a regular nest-dwelling species in Britain, although its larvae have been found in nests in small numbers on several occasions. Its position is discussed later in this paper.

*Records.* Sparrow (2 nests), eaves of house, Upton Park, Slough, Bucks, 4 Aug. 50, SN; sparrow (2 nests), eaves of buildings, Pest Infestation Lab., Slough, Bucks, 10 Aug. 50, SN & VSN; sparrow, eaves of house, Datchet, Bucks, 23 Aug. 50, VSN; sparrow, crevice in wall of bombed house, Neal Street, Covent Garden, London, 23 Nov. 50, VSN.

*Tinea fuscipunctella* Haw. This is another species which is casually associated with stored products, though it has no economic importance. It was found only twice, once in a sparrows' nest and once in pigeon guano.

*Records.* Sparrow, eaves of house, Wallington, Surrey, 29 Aug. 50, VSN; pigeon (many nests), Railway Docks, Brentford, Middx., 15 Nov. 50, VSN.

*Tinea pallescentella* Staint. The Large Pale Clothes Moth is rather more important as a domestic nuisance than the previous species. It was found in considerable numbers in pigeons' nests at Brentford (MN) and Bristol (LN). (Records as for *M. crocicapitella*.)

*Tinea pellionella* (L.). The Case-bearing Clothes Moth is second only to *Tineola bisselliella* as a pest of woollen fabrics. It is abundant and widespread in nests, especially those of jackdaws and pigeons.

*Tinea columbariella* (Wocke). This species also has case-bearing larvae and in the past has probably been confused with *T. pellionella*. It has been found attacking clothing in company with the previous species (Woodroffe, 1950), but the extent to which it is a clothes moth is not yet known. It is very widespread in nests and is usually the dominant species in sparrows' nests.

## Coleoptera.

DERMESTIDAE.

*Dermestes lardarius* L. The Bacon Beetle is a common minor pest of animal products. It occurs widely in pigeons' nests in London, but the record quoted is the only occasion when it was found elsewhere.

*Record.* Sparrow, eaves of house, Wallington, Surrey, 29 Aug. 50, VSN.

*Attagenus pellio* (L.). The Fur Beetle is a clothing pest of some importance. It occurs frequently in nests, and is sometimes very abundant, particularly in jackdaws' nests. It appears less dependent upon the presence of buildings for reaching high population densities than many of the other nest species (see record below). When a dry nest is abandoned by the birds and never used again, it becomes slowly converted into a mass of fine dust (mostly insect faecal pellets) in which the coarser fibres (*e.g.*, straw) remain. Nests in this condition rarely contain much life, but when insects are present, *A. pellio* is usually dominant. It appears to be able to utilise material which has become unsuitable for most other species.

*Record.* Jackdaw (several nests), hollow tree in meadow land, East Bergholt, Suffolk, 5 Oct. 50, VLN.

*Megatoma undata* (L.). This Dermestid is usually found under the bark of trees feeding on the remains of dead insects. It has been known to damage hides. Larvae were found in a nest on one occasion.

*Record.* Robin, in shed, Pest Infestation Laboratory, Slough, Bucks, 28 Oct. 51, SN.

*Anthrenus verbasci* (L.). The Varied Carpet Beetle is a domestic clothing pest that seems to be increasing in importance in many areas. It is a common nest species, but is practically confined to those of sparrows, martins and swallows.

*Anthrenus fuscus* Oliv. This species is only a very minor pest; it seldom occurs in nests, and was found in them on only two occasions.

*Anthrenus museorum* (L.). The Museum Beetle is best known for its depredations in insect collections, although *A. verbasci* is probably as important in this respect. Larvae were only occasionally found in nests, usually in company with those of *A. verbasci*.

(The whole problem of the comparative distribution of these three species of *Anthrenus* is now under examination. By collecting adults from flower-heads in summer some evidence has already been obtained of differences in distribution which can be attributed to differences in type of locality (*e.g.*, suburban areas as opposed to rural areas). By collecting larvae from a variety of situations, in addition to birds' nests, some evidence of differences in larval habitat has been obtained. This work is still in progress and will be reported in a separate publication which will include detailed records of *Anthrenus* in nests.)

CUCUJIDAE.

*Oryzaephilus surinamensis* (L.). This major pest of grain was once found in numbers in sparrows' nests on an Essex farm. Only adults were present, and there was no evidence that breeding took place, or that the species overwintered successfully in this habitat. The insects had probably spread from some infested feeding-stuff, but, from the numbers present, it appeared that they had been attracted to the nests. Infested nests were found in a number of separate buildings on the farm.

*Ahasverus advena* (Waltl.). This species is a minor pest of a very wide variety of materials. It was found only once in nests.

*Record.* Pigeon (many nests), Railway Docks, Brentford, Middlesex, 15 Nov. 50, SN.

ANOBIIDAE.

*Stegobium paniceum* (L.). The Biscuit Beetle is a pest of some importance. It attacks a wide variety of both animal and vegetable products, and frequently causes damage to herbarium specimens. It was one of the dominant species in pigeons' nests in London, but was only once found in nests of other birds.

PTINIDAE.

*Mezium affine* Boie. This species is one of the rarer Ptinids, and is seldom found in any numbers on stored products. It occurred only twice in nests and on each occasion there was an obvious nearby source of the insects. It cannot be regarded as a typical nest species in Britain.

*Records.* Sparrow, ventilator, Parrot House, Regent's Park, London, 29 Sep. 50, VSN; pigeon (many nests), Railway Docks, Brentford, Middlesex, 15 Nov. 50, VSN.

*Trigonogenius globulus* Sol. This minor pest of grain and cereal products was confined to pigeons' nests in London and Bristol, where it occurred in large numbers.

*Records.* Pigeon, under 5th floor balcony, Strand, London, 31 Oct. 50, SN; pigeon (many nests), behind masonry, front of Charing Cross Station, London, 31 Oct. 50, VLN; pigeon (many nests), old sack hoist, clothing store, Peckham Rye, London, 31 Oct. 50, VLN; pigeon (four nests), on beams in transit sheds, Portishead Docks, Somerset, 19 Apr. 51, SN; pigeon (many nests), bombed storage shed, Bristol, 18 Apr. 51, VLN.

*Niptus hololeucus* (Fald.). The Golden Spider Beetle is a common domestic pest, occurring in private houses in small numbers, and occasionally giving rise to major warehouse infestations. It occurred sporadically in nests in small numbers, and the adults show a peculiar preference for rubbish such as mortar rubble, which is often closely associated with some nests, rather than for the nests themselves. Large numbers of adults (mostly dead) were found in such circumstances near jackdaws' nests high up on the roof of Canterbury Cathedral.

*Pseudeurostus hilleri* (Reitt.). This is an introduced but established species which occurs on stored products, principally in the north of the country. It was found in a nest once.

*Record.* Pigeon, on beams outside warehouse, Birkenhead, Cheshire 31 Dec. 51, VSN.

*Ptinus fur* (L.). This species, the White-marked Spider Beetle, is more widely distributed in nests than any other species of Ptinid. The extent to which this may be attributed to its ability to fly is discussed in a later section. It occurs widely on stored products but is of minor importance only. The record quoted illustrates its presence in areas far removed from buildings.

*Record.* Shelduck, on ground under hawthorn bush (*Crataegus*) in meadow, East Bergholt, Suffolk, 5 Oct. 50. VSN.

*Ptinus pusillus* Sturm. This occurs in warehouses in small numbers, usually in company with *P. fur*, and its distribution in nests is similar. In one remarkable instance, a pigeons' nest which was taken from a building in the centre of Maidstone, Kent, and consisted of no more than a handful of twigs and a few lumps of guano, contained 130 adults of *P. pusillus*. No other species of Ptinid was present.

*Records.* Sparrow (2 nests), eaves of house, Slough, Bucks, 14 Aug. 50, SN; swallow (2 nests), outhouse of farm, Wickham Bishops, Essex, 12 Sept. 50, VSN; swallow (2 nests), farm, Stanwellmoor, Middx., 11 Oct. 50, VSN; sparrow, byre of farm, Wickham Bishops, Essex, 29 Apr. 50, VSN; house-martin (2 nests), eaves of house, Nursling, nr. Southampton, 19 Jan. 51, VSN; pigeon (4 nests), on piles of derelict wharf, Portishead Docks, Somerset, 19 Apr. 51, SN; pigeon (many nests), bombed storage shed, Bristol, 18 Apr. 51, SN; sparrow, eaves of house, Canterbury, Kent, 27 Nov. 51, VSN; pigeon, eaves of Coach Museum, Maidstone, Kent, 27 Nov. 51, VLN; jackdaw (many nests), roof of nave, Canterbury Cathedral, Kent, 27 Nov. 51, MN.

*Ptinus subpilosus* Sturm. This is a rare species, and its association with stored products is doubtful. Single specimens were found in nests on two occasions.

*Records.* Sparrow, eaves of house, Wallington, Surrey, 29 Aug. 50, VSN; shelduck, on ground under hawthorn bush (*Crataegus*) in meadow, East Bergholt, Suffolk, 5 Oct. 50, VSN.

*Ptinus tectus* Boie. The Australian Spider Beetle is the most important Ptinid pest in Britain. It is one of the dominant species in pigeons' nests and

occurs also, but less commonly, in sparrows' nests. Its status will be discussed more fully later in this paper.

*Ptinus sexpunctatus* Panz. This is a rare insect, usually associated with bees (Linsley, 1944). It is the only Ptinid which flies freely in this country. Occasional specimens have been found in nests, and in one locality (Bedford) it was abundant (see also pp. 760–761).

*Records.* Sparrow, eaves of house, Addiscombe, Surrey, 29 Aug. 50, VSN; sparrow, eaves of house, Bedford, 5 Sept. 50, LN; sparrow (4 nests), eaves of house, Bedford, 5 Sept. 50, MN; house-martin (4 nests), eaves of house, Bedford, 5 Sept. 50, LN; sparrow, eaves of Flatford Mill, Suffolk, 6 Oct. 50, VSN; house-martin (2 nests), eaves of house, Nursling, nr. Southampton, 19 Jan. 51, VSN.

TENEBRIONIDAE.

*Tenebrio molitor* (L.). The Yellow Meal Worm is rarely more than a nuisance on cereals. It is an important nest species and is widely distributed; it reaches its peak abundance in pigeons' nests.

*Tenebrio obscurus* Fab. The Dark Meal Worm occurred once in a sparrows' nest on an Essex farm. It has a similar status as a pest to *T. molitor* but is much less common.

*Trox scaber* (L.). This species is best known as an inhabitant of owls' nests, and it has been found associated with jackdaws. It sometimes occurs in slaughterhouse waste.

The following species of Coleoptera belonging to several families have been found in nests, mostly in pigeons' nests. They are probably all mycetophagous and are widely distributed in haystacks and vegetable refuse of many kinds. They are all associated with stored products, where they feed on moulds in damp corners of warehouses, or on the products themselves where these have been allowed to become mouldy. They are of no economic importance and differ from typical dry-nest species in their wide distribution elsewhere in a variety of habitats. Consequently they are merely listed here, without individual records.

CRYPTOPHAGIDAE.

*Henoticus californicus* (Mann.), *Cryptophagus scanicus* (L.), *C. saginatus* Sturm., *C. subfumatus* Kraatz., *C. scutellatus* New., *C. distinguendus* Sturm. (including *umbratus* Erich.), *C. pallidus* Sturm., *C. acutangulus* Gyll., *C. cellaris* (Scop.) and *C. postpositus* Sahl.

LATHRIDIIDAE.

*Lathridius bergrothi* Reitt., *Enicmus minutus* (L.), *Cartodere filiformis* (Gyll.), *C. ruficollis* (Marsh.), *Corticaria pubescens* (Gyll.), *C. fulva* Com., *C. crenicollis* Mann., *Corticarina gibbosa* (Herbst) and *C. fuscula* (Gyll.).

MYCETOPHAGIDAE.

*Mycetophagus quadripustulatus* (L.).

COLYDIIDAE.

*Murmidius ovalis* (Beck).

ENDOMYCHIDAE.

*Mycetaea hirta* (Marsh).

**Diptera.**

In general, Diptera are not typical members of the dry-nest fauna. They require moist conditions and are more frequent in the wet type of nest. Those that were found were mostly confined to pigeons' nests and especially to those in which some excess moisture occurred. *Fannia canicularis* was apparently the only species which could tolerate the humidity conditions of sparrows' nests, and it was found only occasionally and in small numbers in such situations. The infrequency with which most of the Diptera have been recorded is also due to the fact that larvae are difficult to rear, and usually cannot themselves be identified beyond the family or genus.

ANISOPODIDAE.

*Anisopus fenestralis* (Scop.) was found once in a flycatchers' nest.

SCATOPSIDAE.

*Scatopse notata* (L.) was bred once in some numbers from a sparrows' nest from London.

HELOMYZIDAE.

*Tephrochlamys tarsalis* Zett. This carrion fly is one of the commonest Diptera found in wet nests, and occurred frequently and in moderate numbers in pigeons' nests.

CALLIPHORIDAE.

*Sarcophaga barbata* Thoms. This common flesh fly is frequently found indoors, but is of little economic importance. It is widespread and sometimes abundant in pigeons' nests.

*Calliphora erythrocephala* (Meig.). This is one of the "blowflies" and has considerable importance in slaughterhouses and wherever food is exposed to it. It is fairly widespread in pigeons' nests.

*Pollenia rudis* Fab. The Cluster Fly was recorded twice from house-martins' nests.

MUSCIDAE.

*Musca domestica* L. Conditions in dry nests are fortunately seldom suitable for larvae of the Common House-fly. It was found on only two occasions, in each case in a house-martins' nest. Only small numbers were present.

*Fannia canicularis* (L.). The Lesser House-fly is the commonest species of Diptera occurring in dry nests. It was found in sparrows' nests, but reached its peak abundance in pigeons' nests, of which it was one of the characteristic species. It has not the medical importance of the Common House-fly.

*Helina uliginosa* (Fall.) was found occasionally in pigeons' nests in London.

*Anthomyia pluvialis* (L.) was found once in a sparrows' nest in London.

**(c) Predators and Parasites.**

**Hemiptera.**

REDUVIIDAE.

*Empicoris culiciformis* (Deg.). This bug occurs in warehouses as a predator of small insects and, probably, mites. It has seldom been reported as it is very difficult to see, and even when observed could be easily mistaken for a mosquito.

It is probably commoner than the records indicate. It sometimes occurred in sparrows' nests.

*Records.* Sparrow, eaves of building, Pest Infestation Laboratory, Slough, Bucks, 10 Aug. 50, VSN; sparrow, eaves of house, Datchet, Bucks, 23 Aug. 50, VSN; sparrow, eaves of old water tank, Regent's Park, London, 29 Sept. 50, VSN; sparrow, under sack hoist, Flatford Mill, Suffolk, 5 Oct. 50, VSN; sparrow, stables, farm, Witham, Essex, 29 Nov. 50, VSN.

*Reduvius personatus* (L.). This was an uncommon species in nests; it is now found as a general warehouse predator, though seldom in large numbers. It occurred in a derelict theatre at Guildford, Surrey, in association with pigeons. The record quoted below is of special interest as being one of the rare occasions on which *R. personatus* has been found breeding out of doors. The specimen found was a nymph, probably in the second instar.

*Record.* Jackdaw, hollow tree in meadow land, East Bergholt, Suffolk, 5 Oct. 50, VSN.

ANTHOCORIDAE.

*Lyctocoris campestris* (Fab.). This bug is the commonest predator found in nests and in warehouses. It is also widely distributed in a variety of other habitats, such as haystacks. In dry nests, it feeds principally upon House-Moth larvae.

## Coleoptera.

HISTERIDAE.

Beetles of this family are often associated with birds' nests in the open, but only in the moister of the dry nests, usually in those of pigeons. Little is known of their habits, but they are probably predatory. All those named below have been found in nests and are also associated with stored products under damp conditions—*Gnathoncus rotundatus* (Kuge.), *Dendrophilus punctatus* (Herbst), *Carcinops quattuordecimstriata* (Steph.) and *Hister merdarius* Hoff.

## Diptera.

SCENOPINIDAE.

*Scenopinus fenestralis* (L.). Larvae of the Window Fly are second in importance only to *Lyctocoris* as both nest and warehouse predators.

## Hymenoptera.

BRACONIDAE.

*Apanteles carpatus* (Say). This species is a common parasite of the case-bearing Tineid moth larvae (see Woodroffe & Southgate (1951b) ).

*Orthostigma pumilum* (Nees). This Braconid also attacks the *Tinea* larvae, but only rarely.

ICHNEUMONIDAE.

*Stilpnus blandus* Grav. A specimen was bred from a larva of *Fannia canicularis*.

*Metacoelus mansuetor* (Grav.). This species is the commonest parasite of the Tineid case-bearers (see Woodroffe & Southgate (1951b) ).

PTEROMALIDAE.

*Mormoniella vitripennis* (Walk.). This has already been referred to as a common parasite of *Protocalliphora azurea*, one of the bird ectoparasites.

*Dibrachys cavus* (Walk.). This is a cosmopolitan parasite with a wide range of hosts. It was bred in some numbers from two puparia of the Hippoboscid, *Crataerina pallida*, and, on one occasion, from the case-bearing larvae of the moth, *Tinea columbariella*.

### The Mite Fauna.

No claim to have surveyed the mite fauna of dry nests with any great degree of thoroughness is made. The vast numbers of mites which normally occur preclude the examination of all but a very small proportion of the whole. Many species or even genera are indistinguishable unless cleared, mounted and examined under the high power of the microscope. Also, in many groups, identification cannot reliably be carried below the level of family. Consequently it is probable that many species have been overlooked, especially if they were present in small numbers among much larger numbers of a closely similar species.

## (a) Ectoparasites of Birds.

### Parasitiformes.

Laelaptidae.

*Dermanyssus gallinae* (Deg.). This is the common fowl mite and it was present in most nests, often in very large numbers. It may, in its nymphal stages, serve as prey for predatory species but otherwise has no importance in the nest fauna.

## (b) Scavengers.

### Sarcoptiformes.

Tyroglyphidae.

*Tyroglyphus farinae* (Deg.). The Flour Mite is the most important mite pest of stored cereal products. It occurs in nests with moderate frequency and reaches high population densities in some pigeons' nests. The record below indicates its occurrence in areas remote from buildings.

*Record.* Shelduck, on ground under hawthorn bush (*Crataegus*) in meadow, East Bergholt, Suffolk, 5 Oct. 50, MN.

*Tyrophagus tenuiclavus* Zach. This species is somewhat less important than *Tyroglyphus farinae*, and is found principally on materials with a high protein or fat content (Hughes, 1948). It is, however, more abundant in nests, and is often the dominant mite species in pigeons' nests.

*Tyrolichus casei* Ouds. *T. casei* is similar in its food preferences to *Tyrophagus tenuiclavus*, but is of less importance as a pest. It was found occasionally in small numbers in nests.

*Thyreophagus entomophagus* Lab. This mite has been found in small numbers in nests on several occasions. It has been reported from stored cereal products and is known to damage insect collections (Hughes, 1948).

*Mealia* sp. Previously, *Mealia pteronyssina* Berl. has been recorded as one of the dominant nest species. Recently, however, specimens have been submitted to Dr. Cooreman of the Royal Belgian Natural History Museum, Brussels, an authority on the genus, and he is of the opinion that they are of a new species which he has kindly agreed to describe. It occurs in very large numbers in most nests, being usually dominant in sparrows' nests. It appears to be less susceptible to low humidities than the other Tyroglyphids mentioned and was found in some very dry swallows' nests which were otherwise practically devoid of mites.

GLYCYPHAGIDAE.

*Glycyphagus domesticus* (Deg.). This is one of the commonest of the stored-products and domestic mites. It occurs on almost any material in a variety of situations, but has little economic importance. It is more widespread and abundant in nests in general than any other species.

*Glycyphagus ornatus* Kram. This species has occasionally been detected among the *G. domesticus* population. Probably it occurred frequently and was usually overlooked.

*Glycyphagus* n. sp. On several occasions a *Glycyphagus* was found which did not appear to correspond with any of the species described by Hughes (1948). It was conspicuous because of the bright red colour of the lateral vesicles, a feature which appeared to be constant and which was present in all developmental stages. Miss P. L. Robertson, then working at this Laboratory, was of the opinion that it was a new species and her description of it is in preparation. She will also give detailed records of its occurrence.

*Ctenoglyphus plumiger* Koch.

*Ctenoglyphus canestrinii* Arm. These two species have occasionally been found in nests. They occur also in food-storage premises, but are of no importance as pests.

**(c) Predators.**

Of the predatory mites which have been found in nests, only the Cheyletids are of any great importance. The others are chiefly casual predators without any real association with nests.

Because of the difficulty of identification, the " Gamasids " have been treated as a group (although the genus *Typhlodromus* has been repeatedly determined) and, as a group, they have some small significance as general predators in warehouses.

**Parasitiformes.**

LAELAPTIDAE.

*Typhlodromus* sp.

**Trombidiformes.**

BDELLIDAE.

*Bdella* sp.

TYDEIDAE.

*Tydeus* sp.

CHEYLETIDAE.

*Acaropsis docta* (Berl.). This Cheyletid occurs occasionally in stored products. It was found in large numbers in sparrows' nests, and less abundantly in those of the other birds. Its predatory habits will be discussed later with those of the other Cheyletids.

*Cheletomorpha venustissima* (Koch). A species which is occasionally found on Tyroglyphid-infested products, this predator was found occasionally, and in small numbers, in nests.

*Cheyletia flabellifera* (Mich.). *C. flabellifera* occurs occasionally among the other Cheyletids in nests and was found in some numbers in those that contained much green moss. It has been reported in small numbers on stored products.

*Cheyletus eruditus* (Schr.). This is the commonest predatory mite found associated with Tyroglyphids on stored products. It is widely distributed in nests, often only in small numbers, but was abundant in most pigeons' nests.

*Cheyletus* sp. On one occasion a house-martins' nest from Bedford was found to be swarming with large Cheyletids which were engorged with blood. It has so far proved impossible to determine the species.

CUNAXIDAE.

*Cunaxa capreolus* (Berl.). This and the next species were found frequently, though in small numbers, particularly in sparrows' nests.

*Cunaxa setirostris* (Herm.).

TROMBIDIIDAE.

*Trombidium* sp.

PSEUDOSCORPIONS.

*Chernes* sp. occurred frequently in nests, often in very large numbers.

*Chelifer cancroides* (L.) was abundant in some pigeons' nests.

Both were probably predatory upon mites or the young larval stages of insects.

## THE ECOLOGY OF THE NEST FAUNA.

### The Dry Nest Habitat.

PHYSICAL CONDITIONS.

*Humidity conditions.*

A bird's nest that is subject to saturation by water undergoes rapid bacterial and fungal decomposition and has a fauna similar to that of decaying vegetable matter in a wide variety of situations. Nests built in the open show these features after they have been abandoned by the birds. On the other hand, a nest that is protected from rain or drainage water decomposes comparatively slowly, and the scavenging fauna of insects and mites that it supports differs widely from that of the wet, exposed type. Nests that are usually dry include those of the house-sparrow (*Passer domesticus*), house-martin (*Delichon urbica*), swallow (*Hirundo rustica*), swift (*Apus apus*), starling (*Sturnus vulgaris*), jackdaw (*Corvus monedula*), and city pigeon (*Columba* sp.). It must, however, be emphasised that it is the position of the nest, and not the species of bird that determines the type. Of the birds named, most habitually build in sheltered situations, but when a house-sparrow, for example, builds in a tree, the nest, with its scavenging fauna, is of the wet type. Similarly, the insect and mite fauna of a blackbird's nest, which is normally of the wet type, includes many dry-nest species if the bird builds its nest in a shed. It is greatly to be regretted that almost all the records of insects taken from birds' nests, while including information as to bird species, make no mention of the position or condition of the nest. Dry examples of nests of the following birds that normally build their nests in exposed situations have been examined: blackbird (*Turdus merula*), robin (*Erithacus rubecula*), spotted flycatcher (*Muscicapa striata*), blue tit (*Parus caeruleus*), tree-creeper (*Certhia familiaris*), wren (*Troglodytes troglodytes*), redstart (*Phoenicurus phoenicurus*), pied wagtail (*Motacilla yarrellii*), and shelduck (*Tadorna tadorna*). It is impossible to draw a precise line between the two nest types. In many nests intermediate conditions are found, and here a mixture of the more tolerant insect species of both groups occurs. Also, some species (*e.g.*, *Monopis rusticella*) are found in both of the extreme types, although, when this occurs, there is usually a marked preference for one or the other.

Finally, it must be emphasised that the terms " wet " and " dry " are relative only. The relative humidity within a nest may be constantly near saturation, but if liquid water is never present in appreciable quantities the nest is of the dry type.

*Temperature conditions.*

It seems unlikely that temperature has any decisive effect upon the nest fauna. While the nest is in use, particularly when the brood is present, its temperature will be considerably higher than that of its surroundings, and there will be no nocturnal fall. These conditions will enable many species to develop rapidly, but once the nest has been abandoned by the birds, temperature conditions will revert to normal, and only those species that can overwinter in the open will survive. It is possible that less hardy species could survive in nests of sparrows and pigeons as these birds often use their nests for roosting throughout the year. In these nests, also, species without a winter diapause would be capable of fairly rapid development during the winter.

THE COMPOSITION OF THE NESTS.

The nest materials comprise organic matter of both animal and vegetable origin. Those of the exposed nest, once it has been abandoned by the birds, are subject to alternate desiccation by sun and wind and saturation by rain. Under these conditions the nest is rapidly reduced to a mass of humus bound together by the coarser fibrous materials. Very soon most of the finer material is washed out by rain, and only the fibre remains. On the other hand, the materials that compose a sheltered nest decompose so slowly that they persist in their original condition for considerable periods and can consequently form a source of food for a more or less permanent population of those insects and mites that are able to thrive on dried organic materials.

## The Dry Nest Community.

It is convenient to make an ecological classification of the insects and mites that breed in nests by considering their methods of obtaining food.

The ectoparasites of the birds are entirely dependent upon them for food and they are of importance in the nest fauna only in so far as they form the prey of predatory species.

The scavengers, with which are included the mycetophagous species, form the largest and most important group. They feed upon the nest materials, the excrement and other waste products of the birds, or upon moulds growing on these materials. The larvae of fleas must be considered as belonging to this group although the adults are entirely ectoparasitic.

The third group consists of insects and mites that are predatory or parasitic upon other nest inhabitants, and this class includes the parasitic Hymenoptera.

If the bird ectoparasites are ignored, the dry-nest fauna consists of scavengers of dried organic materials and their natural enemies. This community can be divided into three groups according to the status in the nest. Group I consists of typical nest-dwelling species. Group II comprises species that are occasional nest-dwellers; that is, they occur infrequently, but may breed successfully if they are able to reach the nest, or when particular conditions prevail. Group III includes the casual visitors, species whose status is doubtful, and those of wide distribution that inhabit the nests only incidentally as an extension or a part of their usual habitat. This classification of species is given in Table II.

The species in Group I are those that truly characterise the dry-nest community. Such a group of species occurs in no other natural habitat in this country, although fragments of it occur in such situations as the nests of rodents

TABLE II.

Classification of dry-nest species according to status.

| | GROUP I<br>Regular inhabitants | GROUP II<br>Occasional inhabitants | GROUP III<br>Incidental inhabitants, casual visitors, and species of doubtful status |
|---|---|---|---|
| Insects—<br>Scavengers—<br>Various orders .. | | *Lepisma saccharina* | Collembola<br>Psocids<br>Isopods<br>Dermaptera |
| Lepidoptera .. .. | *Hofmannophila pseudospretella*<br>*Endrosis sarcitrella*<br>*Tinea pellionella*<br>*Tinea columbariella* | *Monopis crocicapitella*<br>*Tinea pallescentella* | *Ephestia elutella*<br>*Pyralis farinalis*<br>*Monopis rusticella*<br>*Monopis weaverella*<br>*Tineola bisselliella*<br>*Tinea fuscipunctella* |
| Coleoptera .. .. | *Attagenus pellio*<br>*Anthrenus verbasci*<br>*Ptinus fur*<br>*Ptinus tectus*<br>*Tenebrio molitor* | *Dermestes lardarius*<br>*Megatoma undata*<br>*Anthrenus fuscus*<br>*Anthrenus museorum*<br>*Stegobium paniceum*<br>*Ptinus pusillus*<br>*Ptinus sexpunctatus* | *Oryzaephilus surinamensis*<br>*Ahasverus advena*<br>Cryptaphagidae<br>Lathridiidae<br>Other Ptinidae<br>*Tenebrio obscurus*<br>*Trox scaber* |
| Diptera .. .. | *Fannia canicularis* | *Calliphora erythrocephala*<br>*Sarcophaga barbata* | *Tephrochlamys tarsalis*<br>Other Diptera |
| Predators .. .. .. | *Lyctocoris campestris*<br>*Scenopinus fenestralis*<br>*Apanteles carpatus*<br>*Metacoelus mansuetor*<br>*Mormoniella vitripennis* | *Empicoris culiciformis* | *Reduvius personatus*<br>*Orius majusculus*<br>Staphylinidae<br>Carabidae<br>Histeridae<br>Other Hymenoptera |
| Mites—<br>Scavengers .. .. .. | *Tyroglyphus farinae*<br>*Tyrophagus tenuiclavus*<br>*Mealia* sp.<br>*Glycyphagus domesticus* | *Tyrolichus casei*<br>*Glycyphagus ornatus*<br>*Glycyphagus* sp.<br>*Ctenoglyphus* spp. | *Thyreophagus entomophagus* |
| Predators .. .. .. | *Acaropsis docta*<br>*Cheyletus eruditus* | *Typhlodromus* sp.<br>Tydeidae<br>*Cheletomorpha venustissima*<br>*Cheyletia flabellifera*<br>*Cunaxa* spp. | Other Gamasids<br>*Bdella* sp.<br>Trombidiidae |
| Other Arthropoda .. .. | | Pseudoscorpions | Spiders<br>Centipedes |

and social insects and beneath the bark of trees. In unexploited countryside the distribution of the community corresponds with the distribution of the dried organic material upon which it subsists, and this is scanty and discontinuous, forming small, widely separated pockets. Except when they are associated with buildings, birds' nests in our climate are rarely dry. Even when situated in holes in trees, the nests tend to be intermediate in type, some part usually being affected by seepage of rain water. Probably only house-martins' nests, situated under cliff ledges, and the nests of swifts and jackdaws, in crevices and fissures in the rock, are sufficiently protected to provide, occasionally, a really dry nest. Before this community was affected by human activity many of its constituent species must have been rare insects, and this is still true of the entirely rural parts of the country. In his " Preliminary List of the Coleoptera of Windsor Forest " (1939), Donisthorpe says of *Attagenus pellio*: " In cut grass; very scarce." (The cutting of the grass was presumably a human activity.) Of *Anthrenus verbasci* he remarks that the species was taken " once, by sweeping flowers ". He does not record *Ptinus fur* or *Dermestes lardarius* at all, and records *Tenebrio molitor* only in association with buildings. The effect of urban development upon this local and closely circumscribed community has been profound. The buildings of our towns and farms provide dry nesting sites for a vast population of birds, and this considerable food supply is supplemented by the dried organic matter, in the form of stored food and clothing, which is contained within the buildings. Some buildings are used solely for the purpose of storing such materials, and the development of large towns ensures that the available nesting sites and supplementary food supplies are in close proximity. It is not surprising, therefore, that in built-up areas these originally rare dry-nest species are now common insects. Some of them have become serious pests, and most are now regarded as " indoor " species. In undeveloped rural areas the dry-nest community still exists in small, isolated pockets, but in those parts affected by the builder, the house, warehouse, barn or even the whole town, may be regarded as the unit which the original dry-nest community now occupies.

## The Influence of Bird Species upon Nest Fauna.

The basic materials used for nest construction by the various birds studied in the course of this work are very similar as regards suitability as food for scavenging insects. The nests differ, however, in the proportion of the various materials present, and in certain other important characteristics such as humidity, and these differences are reflected in the composition of the fauna of insects and mites. The following paragraphs indicate the particular features of the nests of each of the more important species of bird that significantly affect the composition of the scavenging population.

*House-sparrow* (Plate XIV, fig. 1).

The house-sparrow's nest has been selected as a typical dry nest, and forms a standard for comparison with other species. It consists of a mixture of vegetable fibre (straw and dry grass), animal material (horse-hair, feathers and excrement) and a fine dust the origin of part of which is obscure, but which includes a proportion of insect faecal pellets. The dust is probably important for mites and the very young stages of insects. Such nests are moderately dry and are usually dominated by the case-bearing Tineid moth, *Tinea columbariella*. The Oecophorids, *Hofmannophila pseudospretella* and *Endrosis sarcitrella*, are also abundant, the former more so than the latter. Dermestid, Ptinid and Tenebrionid beetles are present in moderate numbers. Among the scavenging mites, *Mealia* sp. is dominant, with *Glycyphagus domesticus* abundant and *Tyroglyphus farinae* and *Tyrophagus tenuiclavus* in moderate numbers.

*House-martin* (Plate XV, fig. 2).

The house-martin's nest consists of a mud cup, lined with feathers and dry grass, usually placed close beneath some over-hanging ledge so that the entrance consists of a small hole. The quantity of nest material is small, and the total number of insects found is correspondingly smaller than in the sparrow's nest. The chief difference between the two is that the mud cup usually maintains a higher humidity in the nest of the house-martin than is found in the loosely constructed nest of the sparrow. Consequently, *Hofmannophila* is usually the dominant insect and *Glycyphagus domesticus* or *Mealia* the dominant mite. The *Hofmannophila* larvae certainly burrow into, and appear to feed on, the mud cup as well as the lining. This is probably responsible for the breakdown of many of the nests during the winter.

*City pigeon* (Plate XIV, fig. 2).

The typical city pigeon's nest is formed by a slight depression in a mound of guano with which are incorporated a few feathers and pieces of straw. Often large nesting colonies are formed and used for many years. When this occurs the quantity of material present is extremely large. The important factors, in addition to the bulk of the utilisable material, are its very solid nature, its almost exclusively animal origin and the high humidity, particularly within the larger masses of guano. Typically, dominance is shared by *Hofmannophila*, *Ptinus tectus*, *Stegobium paniceum* and *Tenebrio molitor*, with *Lepisma saccharina* and *Fannia canicularis* usually abundant. *Tinea pellionella* and *Dermestes lardarius* are often present in moderate numbers, but *Anthrenus* spp. are seldom found. Mycetophagous species (*e.g.*, *Enicmus*, *Cryptophagus*) occur more frequently here than in nests of other species. *Tyrophagus tenuiclavus* and *Tyroglyphus farinae* are the dominant mites with *Glycyphagus domesticus* abundant and *Mealia* sp. comparatively scarce. It is noteworthy that *Dermestes*, *Stegobium*, *Fannia* and *Lepisma* have rarely been found in other nests and never in comparable numbers.

*Jackdaw*.

The nest is composed of twigs, with the nest cup lined with dry grass, sheep's wool, pieces of paper and string, and dry rubbish of many kinds. Excrement is absent and there is usually a great quantity of dust. The nest may be situated in a recess in masonry or in a hollow tree. The population of insects and mites is usually sparser than in the nests of the previous species. The most conspicuous insects are *Hofmannophila* and *Attagenus pellio* with *Endrosis*, *Tinea pellionella* and *T. columbariella* abundant and *Ptinus fur* and *Lepisma saccharina* in moderate numbers. *Glycyphagus domesticus* is usually the most abundant mite, with *Mealia*, *Tyroglyphus* and *Tyrophagus* in smaller numbers.

*Swallow* (Plate XV, fig. 1).

The open mud nests of the swallow are usually only scantily lined with dry grass, or occasionally feathers. They are situated on beams in barns or other buildings and are usually very dry, sometimes containing practically no life. The Dermestids, *Anthrenus verbasci* and *Attagenus pellio*, sometimes reach moderate numbers; *Tinea columbariella* is often present, and so is *Hofmannophila* when humidity is high enough. But, in general, swallows' nests cannot compare with those previously described as favourable habitats for insect life. *Glycyphagus domesticus*, *Mealia* and *Tyrophagus* all occur, but seldom in large numbers.

**Predator-Prey Relationships.**

A number of the casual visitors listed in Group III of Table III are predators. They seldom show a marked preference for any particular prey, and exert no significant influence on the nest population. On the other hand, the predators in Group I form an important part of the nest community and, from casual observations made during the examination of nest material, it is possible to give

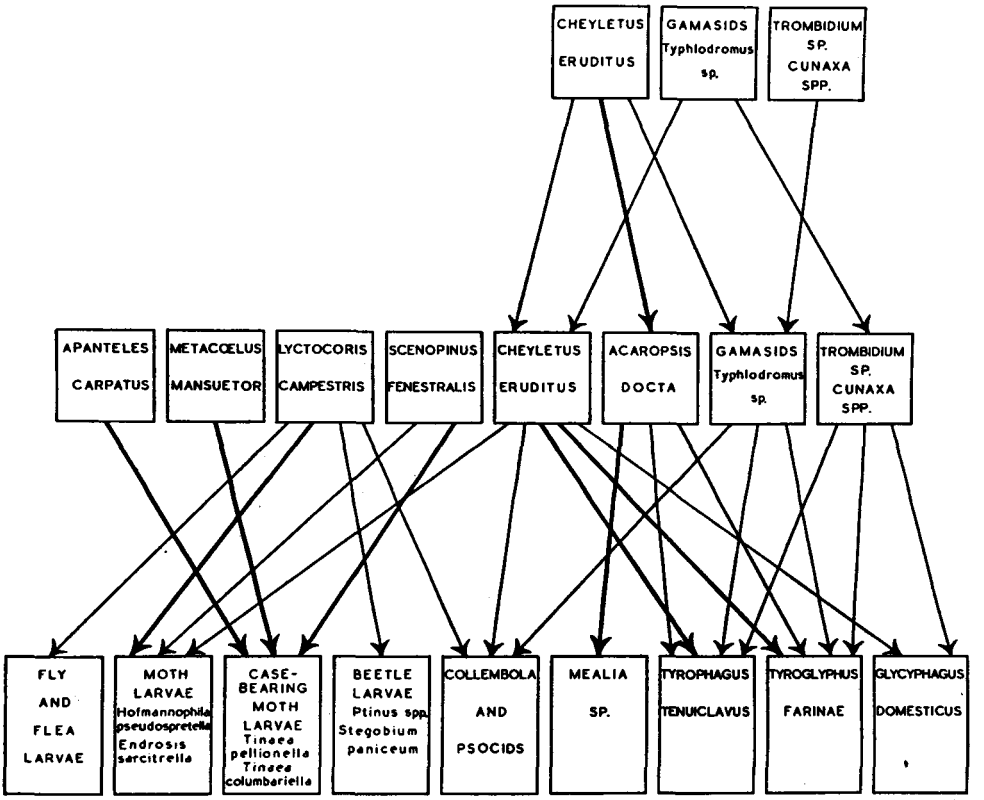


Fig. 2.—Some predator-prey relations within the dry-nest community.

some account of their habits and preferences. Figure 2 illustrates the predator-prey relationships that have been observed. The thick arrows indicate the preferred species of prey when several are available.

*Lyctocoris campestris.*

This is the only predator which has been observed to affect the density of the scavenging population. On several occasions, extreme abundance of this species has been associated with a rather low level of occurrence of the dominant Lepidoptera. The adults and larger nymphs have frequently been observed to feed on *Hofmannophila* and *Endrosis* larvae (see Pl. XVI, fig. 2), and, more rarely, on Ptinid larvae, Collembola, Psocids and fly and flea larvae. Smaller nymphs probably feed on young Lepidopterous larvae and possibly on mites.

*Scenopinus fenestralis.*

The long, thread-like larvae of this fly specialise in attacking the case-bearing Tineid larvae. The Scenopinid larva inserts its head into one end of the case of the

*Tinea* larva to make its attack (see Plate XVI, fig. 1), so taking advantage of the fact that these larvae are usually very reluctant to leave their cases. This habit renders them very susceptible to the attacks of *Scenopinus*. In pigeon nests the case-bearers are often few in number, but the hard lumps of guano are usually riddled with passages made by Ptinid and *Stegobium* larvae. The *Scenopinus* larvae are very suitably shaped for exploring these burrows, and, in these nests, the beetle larvae are probably their chief prey. *Scenopinus* also occasionally attacks the House-Moth larvae. A full-grown *Hofmannophila* larva possesses powerful mandibles which it is not reluctant to use. An attack by *Scenopinus* on a *Hofmannophila* larva which was able to defend itself would probably end in the death of the attacker. However, a successful attack was observed on a larva that had spun up for diapause or pupation. *Endrosis* larvae are less aggressive and are probably more frequent victims.

*Acaropsis docta* and *Cheyletus eruditus*.

The dominant scavenging mite species in sparrows' nests are usually *Mealia* sp. and *Glycyphagus domesticus*. Because of its long setae and rapid movements the latter is not preyed upon to any great extent by Cheyletids. Consequently, *Mealia* must form the staple diet of predators in these nests, and this fact appears to determine the relative abundance of *Acaropsis* and *Cheyletus*. Usually the former is very abundant and the latter comparatively scarce. The explanation seems to lie in the different hunting methods of the two predators. *Cheylatus* prefers to back into some crevice, where it waits, with pedipalps in the attacking position, for something to move within range. It snaps automatically at any moving object, and, unless the attack is successful, runs rapidly backwards and finds another crevice. In contrast to this, it has been observed that the smaller and less aggressive *Acaropsis* uses its pedipalps to examine and turn over small objects. *Mealia* is a small and sluggish mite and *Cheyletus* seldom seems to be aware of its presence, but with its more appropriate method of hunting, *Acaropsis* is able to deal with a prey of this type. Thus, the usual position is that *Acaropsis* preys upon *Mealia* and *Cheyletus* upon *Acaropsis*.

The position is rather different when *Tyroglyphus* or *Tyrophagus* is present. These species are suitable prey for *Cheyletus*, which is consequently very abundant, a state of affairs often found in pigeons' nests. The determining factor is probably humidity. *Tyroglyphus* and *Tyrophagus* require a higher humidity than either *Mealia* or the Cheyletids. A fall in humidity which adversely affected the *Tyroglyphus* would compel the *Cheyletus* to feed upon its own species, and, provided that sufficient *Mealia* were present, the *Cheyletus* would decrease and the *Acaropsis* increase until the position resembled that usual in sparrows' nests.

*Gamasids*.

Predators of the *Typhlodromus* type are often present in moderate numbers in nests. They are usually indiscriminate in their attacks and seem rarely to influence the Tyroglyphid-Cheyletid relationship to any great extent. The outcome of a *Typhlodromus-Cheyletus* battle varies, but the advantage lies most often with the Cheyletid.

## Colonisation of Nests.

One of the major problems facing the nest-inhabiting species is that of reaching the nest. Although many of the nests that are being considered in this paper are used repeatedly, and may last a number of years, the habitat is essentially ephemeral, and reinfestation from outside must be frequently necessary. In many species the adults normally leave the nest, or the larvae

wander away from it before pupation, and consequently reinfestation from outside must normally occur in these species.

Since some species occur in a very high proportion of the nests examined, it seems unlikely that their presence can be entirely fortuitous in all cases. This is particularly true of those nests that possess a small entrance hole. Some mechanism must exist which ensures that a proportion of individuals of these species reach suitable nests. Consideration will now be given to the possible methods by which this may be achieved. Although there is not much positive information, there is a certain amount of evidence upon which tentative suggestions can be based.

*Attraction of flying adults.*

There is some evidence that certain species, the adults of which are capable of flight, possess a definite behaviour pattern, probably based on an olfactory reaction, which enables them to find a nest. A preliminary experiment has been carried out, in conjunction with Mrs. G. M. Blake, of this Laboratory, who is studying the behaviour of *Anthrenus verbasci*. Boxes containing sterilised nest material were erected in pairs on the walls of one of the Laboratory buildings. One box of each pair was protected from crawling insects by a sticky band. All were wired against entry by birds. The nest material was examined at the end of the first summer, and *Hofmannophila*, *Tinea* and *Anthrenus* larvae were present, both in the banded and in the unprotected boxes. A few *Anthrenus* adults were found trapped in the sticky bands. These observations indicate that flying adults of these three species may be attracted to nests. Infestation occurred during the first summer, so the reaction appears to be capable of accounting for a regular annual infestation. These same species were also present in a starlings' nest in a new nesting box at the end of the first season of its use.

In this connection, it is perhaps worth while recording an observation in connection with *Ptinus fur*, a species which, in addition to being widely distributed in birds' nests, is known to breed in nests of bees and wasps (Linsley, 1944). This Ptinid has been observed to fly only very rarely, and such flight as has been observed has usually been more of a controlled fall than " purposeful " flight. The only occasion on which the writer has observed *P. fur* in flight was when a specimen entered the open laboratory window in horizontal flight and alighted on the bench. The time was 9.30 a.m. on a cold but sunny autumn morning when it was surprising to see any species of beetle on the wing. During the previous afternoon, a wasps' nest had been collected for examination, and it was left in the laboratory overnight. The room smelt strongly of it when the window was opened in the morning. This isolated observation cannot be taken as conclusive evidence, but it is certainly suggestive, and it may link up with other similar observations on the olfactory reactions of this species.

*Attraction of crawling adults or larvae.*

This is probably the commonest mode of access of those species that cannot fly. It is likely that the Ptinid beetles, with the exception of *P. sexpunctatus* and possibly *P. fur*, depend upon their climbing powers for reaching nests. It will be seen from Table I that none of the Ptinids occurs with a frequency comparable with that of some of the moths, which fly very much more freely, except for *P. tectus* in pigeon nests, which is a special case and will be discussed later. *P. sexpunctatus*, the only Ptinid which flies at all freely in this country, has, except in one instance, been found only as an occasional individual. It seems unlikely, therefore, that the power of flight alone is a critical factor in determining the distribution of Ptinids in nests. It is possible that *P. sexpunctatus*, which is usually associated with bees, reaches the nests, but finds

the habitat unsuitable; the only available evidence, however, is against this possibility, for *P. sexpunctatus* was present in considerable numbers, and was, in fact, the dominant species of beetle, in eight nests of the house-martin and five of the sparrow from two widely separated localities in Bedford.

The case of *Ptinus tectus* referred to above is one of particular interest. It has been found in 72 per cent. of pigeon nests, where it is usually one of the dominant species. It has been found also in sparrows' nests, often where there appeared to be no obvious source of the infestation. It cannot fly, and was introduced into this country only about fifty years ago. Undoubtedly this is a case where a species was introduced originally into the buildings and has subsequently spread to the nests. Exchange in both directions has probably facilitated the spread of the species. It is generally true that nests in buildings possess a more numerous and varied fauna than dry nests in more isolated situations, and this is doubtless due to the repeated exchange of species between nest and building, each forming a reservoir from which the other may be reinfested. For some species, such as *Anthrenus verbasci*, sparrows' nests probably have a considerable importance as sources of household infestation.

It is instructive to compare the case of the Common Clothes Moth, *Tineola bisselliella*, with that of *Ptinus tectus*. *T. bisselliella* appears, for some reason, to be unable to exploit the nest habitat effectively. In spite of its almost universal distribution in buildings in this country, it has been found in nests only occasionally, and in small numbers, and in most cases there was a very obvious source from which larvae might have crawled. The difficulty appears to be one of access, for the larvae found have been reared successfully on the nest material. In fact these larvae, and the adults reared from them, have been exceptionally large. The indications are of a lack of a suitable behaviour pattern which will enable the adult to reach the nest.

The occasional occurrence of larvae of such species as *Ephestia elutella* in nests can almost certainly be explained by the supposition that they have wandered from some infestation on grain nearby. They have never been found except in very small numbers.

*Conveyance as food by insectivorous birds.*

The possibility cannot be ignored that adult insects of a suitable species may occasionally be carried to the nest as food for the young, and subsequently escape and produce viable eggs. It seems unlikely, however, that such a method of access could have any general importance.

*Conveyance on nesting materials.*

This method is probably of greater importance than the last, and may significantly influence the nest population in certain cases where nest materials are obtained in quantity from infested situations. The presence of considerable numbers of adults of *Oryzaephilus surinamensis* in sparrow nests on an Essex farm can probably be explained in this way. There was no evidence that this species bred or overwintered successfully in this situation. It is very doubtful if any of the more important nest species depend to any great extent on this method.

*Conveyance on the birds themselves.*

This mode of gaining access to nests has been suggested to explain the presence of *Ptinus tectus* in situations apparently inaccessible to it. There are no records of the beetle having been found clinging to birds, but it seems reasonable to suppose that it sometimes reaches pigeons' nests in this way. It has been found in pigeon droppings on high ledges on St. Paul's Cathedral, London, and in nests in a loft at the top of one of the smoke towers of the Natural

History Museum building, South Kensington. It is hard to imagine how such a species could reach these situations except by clinging to the pigeons. No nesting material was used in either case, but pigeons frequently feed and roost in granaries where *P. tectus* is often abundant, and this species appears to be well adapted to clinging to the feathers or feet of a large bird.

Methods 4 and 5 are probably adequate to explain the observed frequency of occurrence of mites in nests. These are much more widely distributed than the insects and, because of their small size, the chances of their conveyance by these methods are greater.

## A Review of the Work of Nordberg (1936).

### Summary of the Work.

The original publication comprises an introduction and six chapters and this arrangement will be retained below.

Introduction.

In his opening statement Nordberg expresses the opinion that previous workers have overstressed the importance of physical factors in determining nest fauna, and have attributed little influence to the host animal.

Chapter I. Methods of investigation.

During the years 1929–33, 422 nests of 56 species of bird were quantitatively examined. Most of the nests were collected in Aland, but some came from the Finnish mainland. There was no selection of material. All nests encountered were examined by means of a Tullgren apparatus. The efficiency of this apparatus was investigated, particularly as regards its lethal effects upon the various groups of arthropods. Enhancement factors, based upon the mortality due to the apparatus, were used in all estimates of population density.

Chapter II. The birds' nest as a biotope.

(*i*) *The nest types.*

The nests are classified according to position: in marshes and floating on water; on the ground; in the open above the ground; in holes and partly in holes. The nests are also grouped as autophagous (from which the young depart soon after hatching) and insessorial (when the young remain in the nest for a considerable period); as excrement-free or excrement-containing; and as annual or perennial.

(*ii*) *Description of the construction and building materials of birds' nests.*

Position and details of construction of the nests are described for each bird species. Also, certain relevant details of the life-histories of the various birds are given, *e.g.*, number of broods, period of occupation, etc. The description of building materials is extremely detailed, all lichens and mosses used being identified.

Chapter III. Systematic list of arthropods found in the nests.

The faunal list includes 528 species of arthropods. Each species is classified as ectoparasitic, zoophagous, necrophagous, coprophagous, schizophagous, phytophagous or indifferent, according to its food preferences, and as eucoene, tychocoene or xenocoene according to its degree of fidelity to the association.

The species are listed in systematic groups and comprise: Isopoda—1; Collembola—21; Dermaptera—1; Psocoptera—13; Mallophaga—26; Hemiptera—6; Neuroptera—1; Coleoptera—116; Lepidoptera—3; Diptera—21; Aphaniptera—23; Hymenoptera—7; Pseudoscorpiones—3; Araneae—11; Parasitiformes—44; Trombidiformes—60; Sarcoptiformes—169.

CHAPTER IV. THE AUTOECOLOGY OF THE NIDICOLES.

Four groups of ecological factors are recognised as affecting the composition of the nest fauna.

(*i*) *General geographical-climatic factors.* These were not considered.

(*ii*) *Local climatic factors.* These include temperature, illumination, relative humidity of the air, relative humidity of the nest material and distance above ground.

Temperature is dealt with in considerable detail. It was measured in various types of nest, in various parts of a nest and at different times during the birds' breeding period. An experimental investigation was carried out to determine the temperature preferendum of some of the nidicoles, and this preferendum is correlated with the temperature of the part of the nest in which a species was usually found. The response of the nidicoles to extremes of temperature was also investigated, in particular the temperature at which they left the nest.

Illumination as a factor affecting the nidicoles was also studied experimentally, and the preferendum was determined for a number of species.

The relative humidity of the air in the nests of several bird species was measured, but was considered to be unimportant in its effects upon the nest inhabitants.

The importance of the relative humidity of the nest materials is discussed in some detail, and was also investigated experimentally, the preferendum being determined for a number of species.

The height of the nest above the ground was found not to influence the composition of the nest fauna.

(*iii*) *Edaphic factors.* The construction of the nest, *e.g.* its texture, and its importance to the nidicoles is considered at a general level.

(*iv*) *Biotic factors.* These are very briefly considered under three headings—nutritional relations, reproductive relations and relations to enemies.

CHAPTER V. THE SYNECOLOGY OF THE NIDICOLES.

(*i*) *Distribution of species, individual and volume quantities of nidicoles among nests of different species of birds.*

The density of habitation per unit volume of nest was estimated both as numbers of individuals and as volume-quantities. Nordberg adopts the latter estimate and gives his reasons for doing so. Tables are given showing density of habitation by nidicoles of the various systemic groups of arthropods in nests of all bird species, and in the four nest groups (aquatic, ground, tree and hole nests), estimated by both methods.

(*ii*) *Distribution of species and volume-quantities of nidicoles among the different nutrition-biological categories.*

In this section the nidicoles are classified according to their feeding habits (as ectoparasites, zoophages, phytophages, etc.). The habits of the different groups are briefly described and tables give volume-quantities of nidicoles, classified in this way, per unit volume of nest for all bird species.

(*iii*) *Distribution of nidicoles in different layers of the nest.*

Ten nests, belonging to two bird species, were examined in three layers, and the layering of nidicole species is correlated with their temperature and food preferenda.

*(iv) Sociological characteristics of the stocks of nidicoles.*

(a) The constancy of species in the nests of different species of birds and in different groups of nests.

Several conceptions of constancy and methods of estimating it are discussed. The following degrees of constancy were recognised:—

Constant species – present in more than 50 per cent. of nests examined.
Accessory species – present in 25–50 per cent. of nests examined.
Accidental species – present in less than 25 per cent. of nests examined.

Lists of constant, accessory and accidental species of nidicole are given for each bird species and for each of the four nest groups.

(b) The dominance of volume-quantities of the species in nests of different species of birds.

Three degrees of dominance were used:—

Dominant species (Dominanten) – volume more than 5 per cent. of the total volume of nidicoles.
Influent species (Influenten) – volume 2–5 per cent. of the total volume of nidicoles.
Recedent species (Rezedenten) – volume less than 2 per cent. of the total volume of nidicoles.

The dominants and influents are listed for each bird species, and the significance of dominance is briefly discussed.

(c) The fidelity of the association of the nidicole stock of the nests.

The ideas of various workers concerning fidelity of association are given and criticised. The classification adopted consisted of the following groups:—

Eucoene species—animals that belong exclusively to the nidicole stock of birds' nests or are found there in larger numbers than in other stocks.

Tychocoene species—animals often or even regularly found in the nidicole stock of birds' nests, but not in such numbers as in other stocks which they prefer.

Xenocoene species—animals which belong to other stocks and are found only by chance in the nidicole stocks of birds' nests.

The distribution of these coenological groups of nidicoles among the nests of different bird species is given in a table and illustrated by a graph. The relative proportions of the groups in different types of nest is considered in some detail and some general conclusions are drawn.

## Chapter VI. The development of the nidicole stocks.

*(i) How the nidicoles reach the nest.*

Four modes of access are suggested—transportation on the nest materials, transportation on the host animal, chance access and deliberate entrance.

The first three methods are mentioned only briefly, but the last was studied experimentally, and the conclusion was reached that some species search actively for the nest and locate it by smell, often over considerable distances.

*(ii) The development of nidicole stocks in nests used for one brood only.*

The time of arrival and departure of the nidicoles is correlated with the breeding cycle of the birds.

*(iii) The development of the stock of nidicoles in perennial nests.*

This was studied by examining samples at intervals during one summer. The samples were taken from a single large jackdaw colony which was regarded as a single homogeneous unit. Graphs are given showing the variation during the summer of the total animal stock and of the relative proportions of species comprising different nutritional categories.

## Discussion of Nordberg's Work.

When reviewing a paper of this size it is necessary, for the sake of brevity, that attention should be largely confined to those points where some disagreement occurs. The above summary has indicated the immense scope of the work, which contains much valuable information and some stimulating ideas, and this must be emphasised in view of the largely adverse criticism that follows.

### I. Methods.

The disadvantages of using automatic methods of separation in order to provide a quantitative estimate of density of habitation have already been considered to some extent. Eggs and pupae cannot be detected by such methods, and there are indications that such groups as lepidopterous larvae are affected by the Tullgren apparatus to a greater extent than Nordberg allowed for by his use of enhancement factors. It is interesting to note that his faunal list includes only three species of Lepidoptera, whereas four species of leaf-eating Chrysomelid beetles, whose presence could only have been fortuitous, were recorded. In Britain, microlepidopterous larvae are usually among the dominant inhabitants of dry nests (Table II gives 12 species), while in exposed nests, such species as *Monopis rusticella* and *Tinea ganomella* Treit. occur in considerable numbers and with very high frequency. While these particular species may not occur in Finland, it is very surprising that 422 nests of 56 bird species contained only three species of Lepidoptera. Also, automatic collection involves killing the insects and this often creates considerable problems in identification. The determination, to species level, of lepidopterous, coleopterous or dipterous larvae is a problem which few specialists in those groups would undertake with confidence. Furthermore, such methods automatically eliminate any chance of detecting the presence of hymenopterous or dipterous parasites of the nidicole species.

### II. The birds' nest as a biotope.

Nordberg classifies nests according to position but he fails to recognise the overriding importance of the degree of exposure to rain. The wet-dry classification is fundamental in the study of nest fauna and the position would be simplified in many ways if these two types of nest were regarded as forming two distinct biotopes. Nordberg's annual-perennial grouping approximates fairly closely to the wet-dry classification, but differs from it in that the perennial nest situated in the open should be regarded as annual in character. Such nests are exposed to the winter weather and are either reduced to a mass of humus or the finer materials are washed or blown away, leaving only the framework of coarse materials to form the foundation of the next year's nest. Consequently they are largely rebuilt each year, though on the same site.

### III. The Faunal List.

While the sheer magnitude of the task of determining accurately such a list of species as Nordberg presents inevitably raises doubts as to the reliability of the more difficult identifications, these must, in the absence of contradictory evidence, be accepted at their face value. Some of the records, especially those of certain ectoparasites, are surprising, but it must be presumed that they reflect existing differences between Britain and Finland.

### IV. Autoecology.

The experimental methods by which Nordberg analysed the response of certain nidicole species to physical conditions appear to be generally sound, although one or two doubtful points should be noted.

*Temperature.*

The gradient used to determine the preferendum was 20–50°C. This was almost certainly too high. Deal (1941) has studied the temperature preferendum of 16 species of stored-products insects. He found that the range of variation in the response to a temperature gradient within one species was very wide, and that changes of behaviour occurred as a result of changes in pretreatment in respect of temperature, food, etc. For example, both with and without food, adults of *Ptinus tectus* showed a preference for about 8°C., at which temperature they were active (*i.e.*, they were not trapped in the cold zone), but on one occasion, when tested without food, they showed a weak preference for 20–25°C. Again, adults of *Anthrenus verbasci* showed a peak preferendum below 15°C., but the range extended as high as 30°C. Some species (*e.g.*, *Stegobium paniceum*) gave evidence of two peaks in their range of temperature preference. Very few of these results would have been evident had Nordberg's range of temperature been used, and several of the species tested by Deal are nidicoles. In the face of such variable and conflicting evidence it is possible to conclude only that the insects tested are highly variable in their response to a temperature gradient, or that the experimental methods used by one or both of these workers were insufficiently refined to demonstrate the preferenda accurately.

*Humidity.*

Nordberg states that he measured relative humidity in the nests of different birds but fails to describe the method used. Also, when studying the effects of extremes of temperature upon the nidicoles, the problem of controlling the relative humidity in the apparatus while the temperature was raised from 0°C. to 60°C. at the rate of 1°C. per two minutes is dismissed by the statement that it was kept unchanged as far as possible. No indication is given of how this was achieved.

A general criticism of this section on autoecology is that several of the most important effects of physical conditions have been overlooked. Throughout his paper Nordberg assumes that nidicole species develop more rapidly and efficiently at moderately high temperatures. This is not universally true. Some species (*e.g.*, *Hofmannophila pseudospretella* and *Anthrenus verbasci*) develop most successfully at comparatively low temperatures. A high temperature may stimulate rapid larval growth but it may also induce a prolonged larval diapause, the final effect being an increased instead of a decreased total development period at the higher temperature. As regards moisture, the most important effect is not the direct effect of humidity upon the nidicole species, but the action of rain upon the nest materials. Nordberg admits that degree of exposure to rain is an important factor controlling the relative humidity of the nest materials, but he fails to realise the primary importance of this factor in determining nest conditions and consequently nest fauna.

V. Synecology.

(*a*) *The advantages of biovolume as an estimate of population density.*

Nordberg adopts the volumetric instead of the numerical estimate of population density because of the considerable size differences between the various species of nest-dwelling arthropods. This method not only takes into consideration the difference in size between an adult mite and an adult insect but also allows for the equally great size difference between a young larval and an adult insect. In the latter instance, it must be remembered that young larvae are potential adults and therefore, in some respects, possess a significance in the population greater than is indicated by their volume. This must obviously be taken into account when considering the degree of dominance of different nidicole

species, and so, for this purpose, biovolume appears to have little advantage over the numerical estimate as a measure of population density. Nordberg's choice of this method indicates what is probably the most important fault in his approach to the problem of the dynamics of the nest population, namely, his static conception of dominance, which permits accurate quantitative analysis but ignores the essentially dynamic conditions within the nest community. This point will be considered in detail later.

(*b*) *The accuracy of the nutritional and coenological classification.*

Every species in the faunal list is classified according to its feeding habits (*i.e.*, as ectoparasitic, zoophagous, necrophagous, coprophagous, schizophagous, phytophagous or indifferent) and its fidelity to the association (*i.e.*, as eucoene, tychocoene or xenocoene). Nordberg writes, concerning the coenological groups, that in a number of instances it was difficult to make a choice between these categories, as the mode of life of the species concerned was not adequately known. In all doubtful cases the category less well defined was chosen. Not only must this proviso apply equally to the nutritional classification, but, in either case, constitutes a very considerable understatement. Nordberg's list of 528 species of arthropods includes a high proportion of little-known species. In respect of these the apparently preferred habitat is probably the only one which has been sufficiently thoroughly investigated to reveal their presence. In the present state of entomological knowledge it is generally true that the known distribution of a little known species or group reflects the distribution and habits of entomologists rather than of insects. The following examples illustrate some of these points.

The Anthocorid bug, *Lyctocoris campestris*, is a common, widely distributed and well known species. In Britain, it has acquired the common name of " Stack Bug " because of its abundance in haystacks. It occurs also in ditches in open country, on rubbish dumps, in birds' nests, in warehouses, etc. It is predominantly carnivorous in Britain, feeding upon other insects and small arthropods, but it has been known to bite humans. The other British Anthocoridae have similar feeding habits. This typical predator is classified by Weidner (1952) as an ectoparasite of birds, and by Nordberg as a phytophage. If there can be such a wide divergence of opinion concerning the feeding habits of such a common species as *Lyctocoris campestris*, Nordberg's classification of the less common species cannot be considered reliable.

Several further examples may be briefly dealt with. Nordberg's description of all the Staphylinidae he lists as zoophages is an unjustified assumption. One of the species he so describes (*Bledius diota* Schio.) almost certainly feeds largely upon algae (W. O. Steel, in litt.). *Nycteribia* sp. is described as tychocoene. The Nycteribiidae are ectoparasites of bats and Nordberg records *Nycteribia* sp. only from sparrows' nests, of which he examined six. *Cheyletus eruditus* is the commonest predatory mite found on stored products. Nordberg records it from nests of one bird species (*Columba oenas*) but classifies it as eucoene.

(*c*) *Constancy.*

Very few of the results of the dry-nest survey in Britain are directly comparable with Nordberg's findings in Finland, but the estimates of constancy for nests of certain bird species may be so compared. The information given in fig. 1 may be expressed according to the degrees of constancy used by Nordberg and compared directly with his results for these insects in nests of the same bird species. Such a comparison, involving, on each side, 115 estimates of constancy, shows that complete agreement on an estimate of " constant " occurred only twice—for *Anthrenus verbasci* in sparrows' nests and for *Fannia canicularis* in pigeon nests. Complete disagreement (*i.e.*, an estimate of

" constant " opposed to one of " absent ") occurred 36 times. This contrast must be attributed to differences in methods and to actual faunal differences between Britain and Finland.

*(d) Dominance.*

Mention has already been made of Nordberg's static view of dominance. He analysed nests by automatic methods and designated species as dominant, influent or recedent according to the proportion of the total volume of life which each represented. For any one nest this method gives a valid estimate of volume dominance at a point in time, but it is inadmissible to draw any general conclusions regarding dominance from such analyses unless adequate numbers of nests of each bird have been examined at different times of the year. Nidicole species differ widely in the details of their life-histories and the pattern of volume dominance is continually changing. Species developing at different speeds reach their maximum biovolume at different times. Some species have one generation a year and some several; the adults of certain species are short-lived, or leave the nest immediately, while others live a long time and remain and feed in the nest; one species may reach the nest early in the year and another later, or the same species may arrive several times at long intervals. Nordberg's nest analyses give a few cross-sections of a complex and dynamic pattern but they give no indication of the complete picture. He justifies his methods by stating that the nidicoles make use of all available means of existence so speedily that the nest, even when perennial, becomes quantitatively and qualitatively saturated during the first summer. This is not true of perennial nests in this country. Some observations on this point are recorded in Section 5 of this paper (Colonisation of nests: (a) Attraction of flying adults) and further observations of a similar nature have confirmed that comparatively few species reach the nest during the first summer of its existance, and that their numbers are small. It seems unlikely that complete qualitative and quantitative saturation is ever reached in perennial nests which are added to annually because of repeated use by the birds. A degree of unsaturation is almost certain to exist as conditions vary and populations fluctuate.

Manual, qualitative examination of nests at different times of the year can give a truer picture of the dominance relations of the nest fauna. Eggs and young larvae, although insignificant in volume at the time of examination, are an indication of a potential future dominance, while larval skins and empty pupal cases may indicate a dominance which would have been obvious had the nest been examined earlier. Also, the presence of certain species, *e.g.*, the parasitic Hymenoptera, cannot be detected by any method of collection that kills the host larvae.

An additional example of the inadequacy of Nordberg's conception of dominance is provided by his view of the importance of recedent species. Nordberg writes that recedent species were not considered as they are unimportant for the evaluation of the conditions governing dominance. That this is not always true is shown by the following example. The presence in a nest of several hundred eggs of *Hofmannophila pseudospretella* suggests that, had the nest been examined three months later, a hundred or so fully-grown larvae would have been found; this is almost certainly a case of dominance by any method of estimation. But *Hofmannophila* has one important enemy, the predatory mite, *Cheyletus eruditus*, which can successfully attack the very young larvae (Woodroffe, 1951) (see Pl. XVI, fig. 3). If this mite happened to be present in some numbers when the *Hofmannophila* eggs were hatching, few of the larvae would be likely to survive, and the potential dominance would not be realised. *Cheyletus* is never present in such numbers as to raise the species above the recedent level of volume, but it may often be an important factor governing dominance in the nest.

(*e*) *The dominance of eucoene species.*

At the end of the chapter on synecology, Nordberg states that the predominance of eucoene groups depends upon the degree of specialisation of the ecological conditions. Earlier in the same chapter, in his discussion of dominance, he writes (to quote the translation): "a species specialized (spezialisierte) for the nest of one particular bird species is best suited to live there. The nests are biotopes of a very specialized (spezielle) kind, conditions of warmth, illumination and humidity differing from nest to nest, and the food is often of a very specialized nature too. A species of nidicole which has its optimum under these conditions will devolop a greater degree of dominance than another less specialized species". He then goes on to quote the opinion of Vestal that moderately specialised species have a greater chance to dominate, and agrees that this may be true of biotopes which are poorly differentiated ecologically, but insists that it is not true of birds' nests.

These generalisations give rise to three important questions:—

(i) What is meant by highly specialised ecological conditions and highly specialised species?

(ii) Is a birds' nest a biotope of a highly specialised kind?

(iii) Are eucoene species dominant in nests and, if so, how may this dominance be explained?

These three questions will be considered in turn and for this purpose Nordberg's results will be accepted at their face value. His conception of dominance, the reliability of his coenological classification and his failure to distinguish the wet- and dry-nest biotopes have already been criticised. What has been said in connection with these points obviously has considerable bearing upon these questions. It is, however, instructive to discuss them without reference to previous arguments.

(i) Unfortunately Nordberg fails to explain what he means by highly specialised ecological conditions. Some definition must therefore be suggested. Highly specialised ecological conditions would seem to require, as a minimum, restricted variability and a considerable degree of peculiarity to the biotope. Precise measurement of degree of specialisation is not possible, but some assessment may be made by considering each individual factor in connection with these minimum requirements for high specialisation. If this tentative definition is accepted then a highly specialised species will be one which is closely adapted to highly specialised conditions.

(ii) Nordberg mentions warmth, illumination, humidity and food as factors determining the degree of specialisation of the ecological conditions of the nest biotope. It is not easy to see how a habitat which provides sustenance for ectoparasites, zoophages, necrophages, coprophages, schizophages, phytophages and indifferent feeders can be considered highly specialised from the nutritional point of view. Similarly, in a single nest, physical conditions vary in different parts and, within one bird species, accidents of position may produce a very wide range of variation. In the face of these facts it does not seem possible to regard the nest biotope as highly specialised ecologically. It seems more satisfactory to regard a nest as an island habitat, distinct from the surrounding environment, but not necessarily more highly specialised.

(iii) Nordberg's results support his contention that eucoene species predominate in nests and he explains this by correlating the degree of dominance with several rather nebulous factors, *e.g.*, the degree of isolation of the nest or nest group and the degree of specialisation of the ecological conditions. Since it has been argued ( (ii) above) that the nest is not a highly specialised habitat, it is necessary to explain the dominance of eucoene species in some other way. For this purpose it is convenient to consider the two nest types, wet and dry, separately.

(a) Wet nests—*i.e.*, annual and exposed perennial nests.

The time available for colonisation of an annual nest is extremely short and in consequence the problem of early access is a vital one for the nidicoles. In this respect ectoparasites have an overwhelming advantage over all other species because they usually arrive in numbers on the host bird, and this one fact may account for their dominance, and therefore a dominance of eucoene species, in annual nests. By the time non-parasitic species reach the nest in any numbers there is insufficient time to allow them to exploit it to any great extent. This explanation of the dominance of eucoene species in annual nests involves no general assumption of a high degree of adaptation to specialised conditions. It is based primarily upon the importance of the time factor where temporary habitats are concerned.

(b) Dry nests—*i.e.*, sheltered perennial nests.

In Britain eucoene species do not predominate in dry nests. The fauna may, in general, be described as specialised in that it consists of species which feed upon dried organic materials, but few could be described as eucoene. Many are well known pests of stored products and are common also in other habitats. Nordberg's conclusion that eucoene species predominate even in perennial nests may reflect a difference between Britain and Finland or it may be due to the several sources of error which have already been discussed. He refers repeatedly throughout his paper to the rapid summer development and winter hibernation of the nidicoles. In dry nests in Britain, the more slowly developing species reach their peak biovolume during the winter. Nidicoles may arrive at the nest at any time between April and September and development of the offspring of the late arrivals takes place slowly during the winter. Nordberg gives no indication that he is aware of the considerable winter populations of many perennial nests. In his last chapter he describes his investigations into the development of the nidicole fauna. He took samples from a jackdaw colony at intervals and analysed them in his Tullgren apparatus, but these observations were continued for one summer only.

**Summary.**

The chief aims of the survey and an important conclusion reached during some preliminary work are briefly stated. This latter was the recognition of two distinct nest types—the wet nest, exposed to rain, and the dry nest, sheltered from rain.

The methods used to examine materials and record results are described. They were closely similar to those described in a previous publication.

The insect fauna is listed under three headings: (a) ectoparasites of birds, which includes 12 species; (b) scavengers, including 66 species; and (c) predators, comprising 14 species. Figures are given for the frequency of occurrence and the abundance of the more important nidicole species, abundance being given as an arbitrary estimate. The importance of each as a pest is also briefly stated, and detailed records are given for uncommon or particularly interesting species.

The mite fauna is dealt with in a similar manner. It includes one ectoparasite, 10 scavengers and 11 predators.

The basic composition of nests and the temperature and humidity conditions within them are described briefly and the possible influence of these factors upon the nest fauna is discussed.

The species of the dry nest community are classified, according to their feeding habits, as ectoparasites of birds, scavengers and predators, and according to their status in the nest, as regular, occasional and incidental inhabitants. The distribution of the group of species which truly characterises this community is discussed.

Differences between the fauna of the nests of different bird species are correlated with differences in the composition of the nests. Certain species were found to be particularly associated with certain nests—*e.g.*, *Tinea pellionella* and *Attagenus pellio* with jackdaws, *Anthrenus verbasci* with sparrows and *Dermestes lardarius*, many Ptinidae, *Stegobium paniceum*, *Lepisma saccharina* and *Fannia canicularis* with pigeons.

Details are given of the more important predator-prey relationships which were observed in the nests. The following cases are considered in detail: *Lyctocoris campestris*, predatory upon House-Moth larvae, *Scenopinus fenestralis* upon larvae of the *Tinea* casebearers, and *Acaropsis docta* and *Cheyletus eruditus* upon several Tyroglyphids.

Possible methods of nest colonisation are discussed: (a) attraction of flying adults; (b) attraction of crawling adults or larvae; (c) conveyance as food by insectivorous birds; (d) conveyance on nesting materials; (e) conveyance on the birds. The modes of access of *Anthrenus verbasci*, *Ptinus fur*, *Ptinus sexpunctatus*, *Ptinus tectus* and *Tinéola bisselliella* are considered in some detail.

Nordberg's " Enquiry into the biology and ecology of the nidicoles of birds " is summarised. This work appears to have been overlooked in the past by reviewers of birds' nest entomology.

A detailed discussion is given of the most important points of disagreement between Nordberg's conclusions and those of this paper. Nordberg's work has three chief faults: (a) His quantitative methods were inadequate in some respects, and there are doubts as to the reliability of his information on the feeding habits and distribution of certain species. (b) Certain fundamental ideas, *e.g.*, the importance of bird species in determining nest fauna and his static conception of dominance, appear to be in contrast to the facts. (c) The use, as key factors in his arguments, of conceptions such as " degree of specialization of ecological conditions " which, in the absence of precise definition, are virtually meaningless, and which cannot be measured or easily assessed.

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Since this manuscript was written, Dr. W. J. Hall, of the Commonwealth Institute of Entomology, has drawn my attention to the following recent publication:—

HICKS, E. A. (1953). Observations on the insect fauna of birds' nests.—J. Kans. ent. Soc., **26,** pp. 11–18.

This paper is of no great importance, but it gives some useful references. In particular, the following two are ecological studies of nest fauna, that of Leleup (1947) being of considerable interest.

HESELHAUS, S. J. (1915). Weitere Beiträge zur Kenntnis der Nidicolen.—Tijdschr. Ent., **58,** pp. 251–274.

LELEUP, N. (1947). Contribution à l'étude des Arthropodes nidicoles et microcavernicoles de Belgique.—Bull. Ann. Soc. ent. Belg., **83,** pp. 304–343.

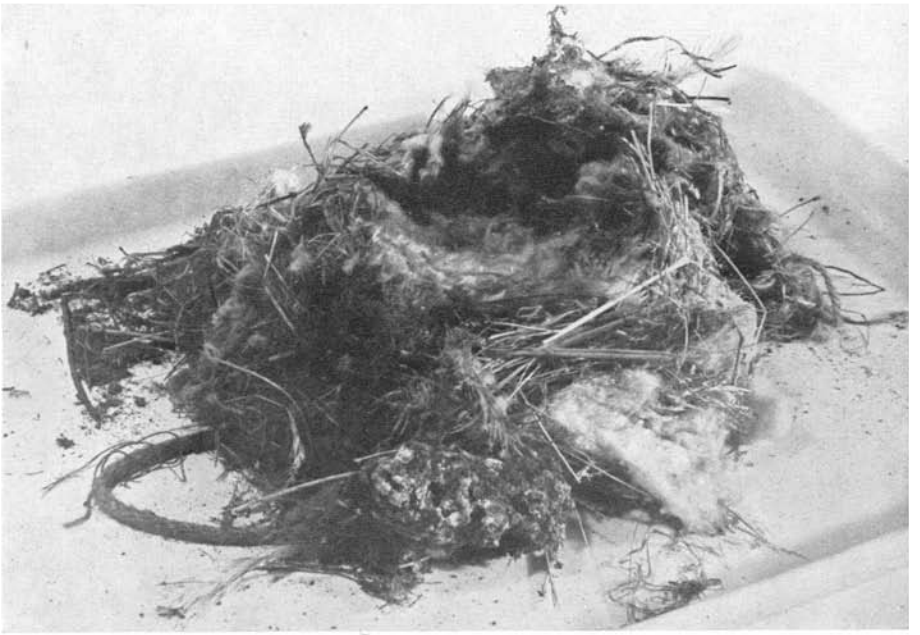

FIG. 1. House-sparrow (*Passer domesticus*).

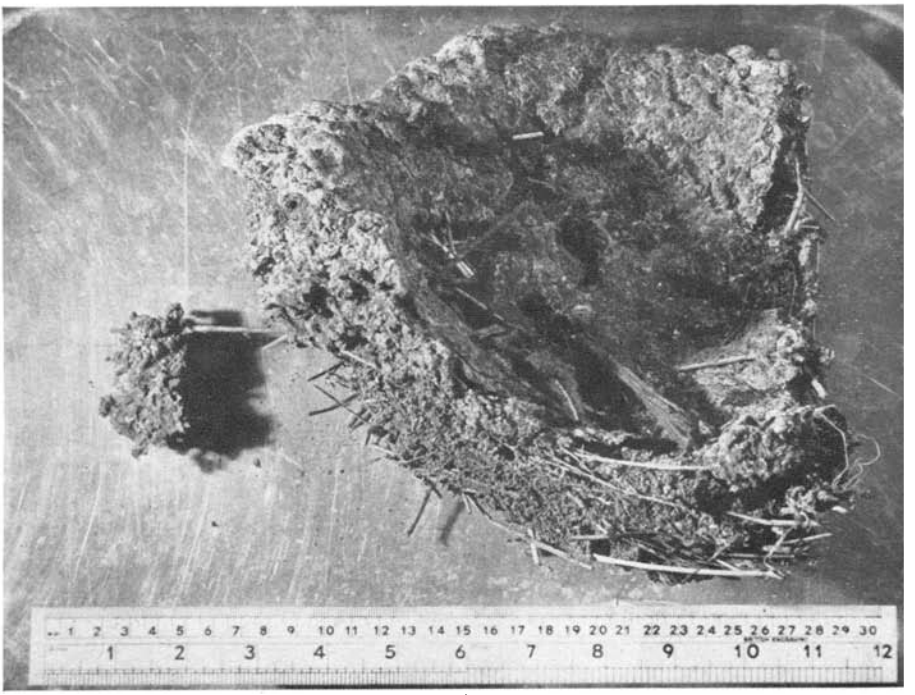

FIG. 2. City pigeon (*Columba* sp.).

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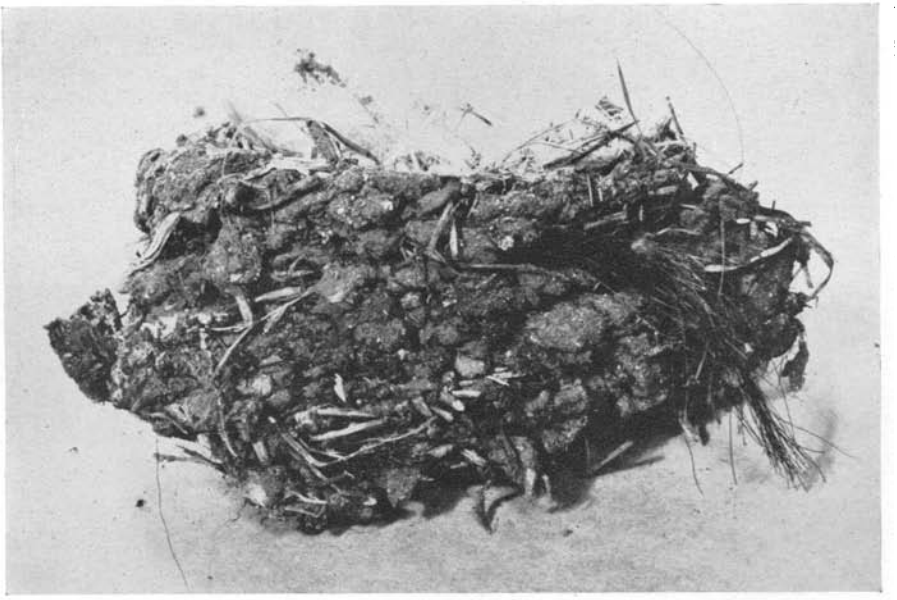

FIG. 1. Swallow (*Hirundo rustica*).

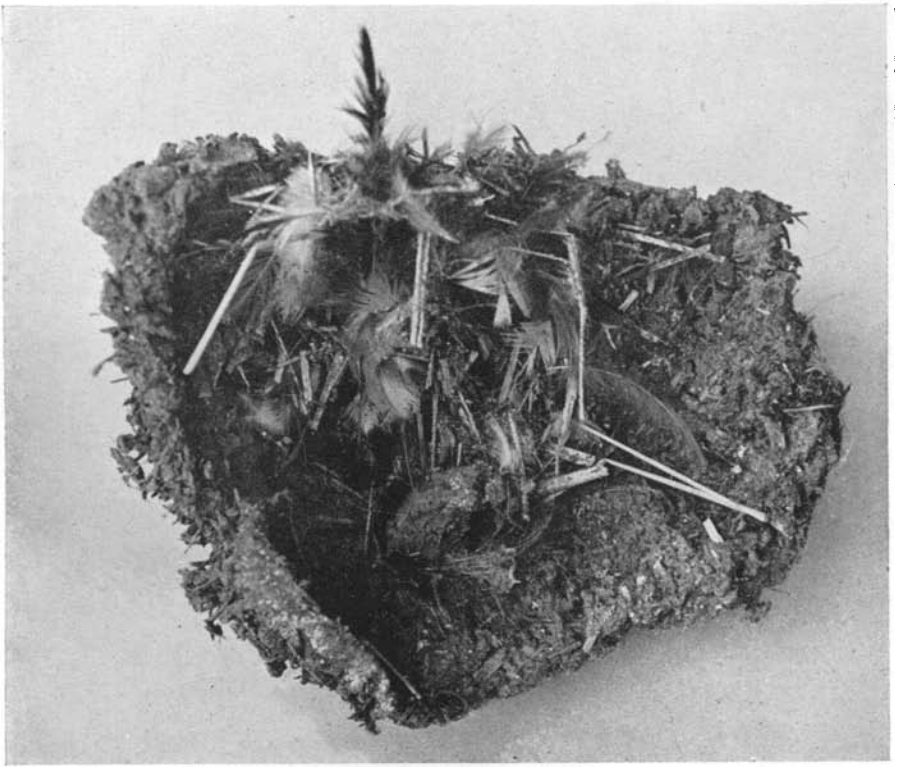

FIG. 2. House-martin (*Delichon urbica*).

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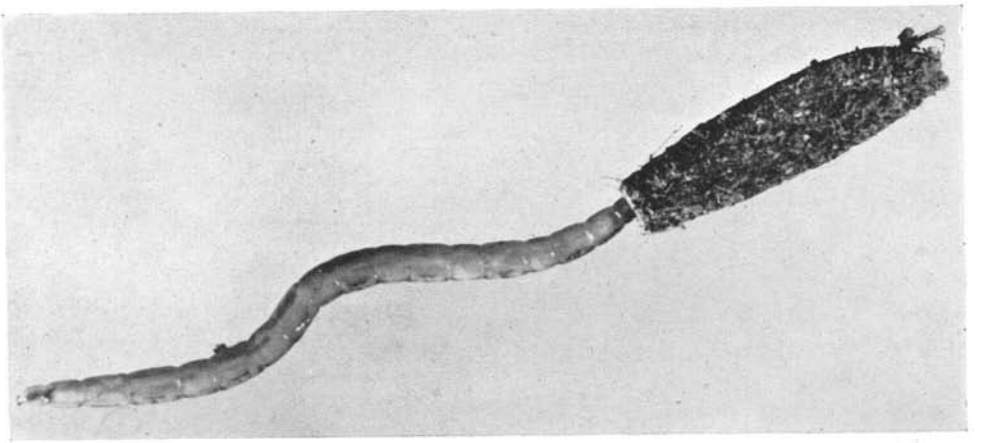

FIG. 1. Larva of *Scenopinus fenestralis* attacking larva of *Tinaea columbariella*.

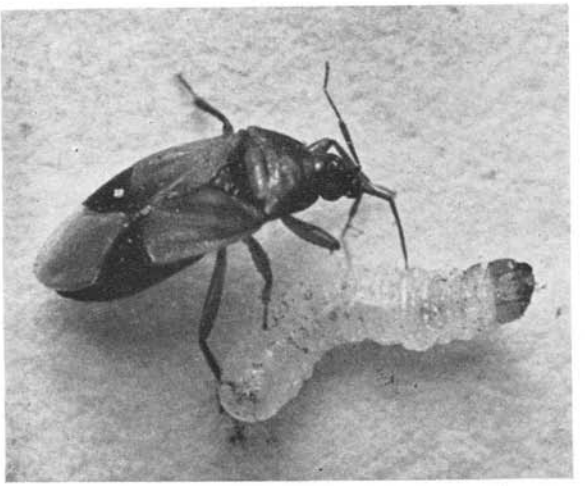

FIG. 2. *Lyctocoris campestris* attacking larva of *Endrosis sarcitrella*.

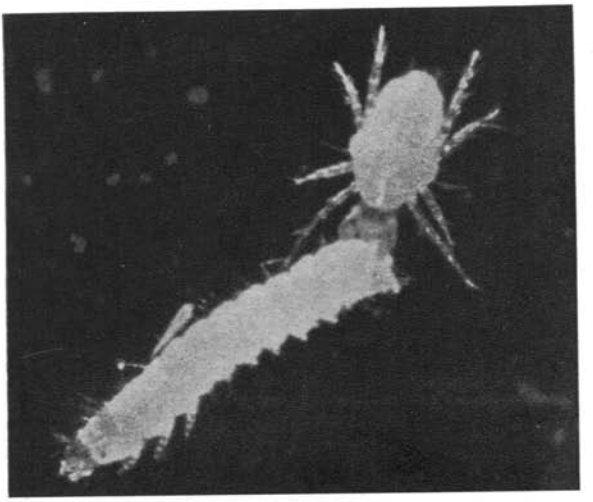

FIG. 3. *Cheyletus eruditus* attacking young larva of *Hofmannophila pseudospretella*.

SOME TYPICAL NEST PREDATORS WITH THEIR PREY.

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