This publication should be cited as:
Campbell, L.H., Avery, M.I., Donald, P., Evans, A.D., Green, R.E., & Wilson, J.D. 1997. *A review of the indirect effects of pesticides on birds. JNCC Report*, No. 227. Joint Nature Conservation Committee. Peterborough

JNCC Report

No. 227

A review of the indirect effects of pesticides on birds

A report to the Department of the Environment and the Joint Nature Conservation Committee (JNCC) through its English Nature lead agency on Toxic Chemicals and Air Pollution. The report was prepared by the Royal Society for the Protection of Birds on behalf of a consortium consisting of Oxford University (BBSRC-NERC Ecology and Behaviour Group), Birdlife International, Butterfly Conservation, the Institute of Terrestrial Ecology, Plantlife and the Royal Society for the portection of Birds.

Copies of this report are available from: JNCC Communications, Monkstone House, City Road, Peterborough PE1 1JY.

Published by the Joint Nature Conservation Committee, Peterborough, UK

JNCC Report, No. 227

ISSN 0963-8091

Chapter 3 The diet of key lowland farmland birds

This section is an edited version of a comprehensive report that was compiled as part of the process of carrying out this Review. The full report (Wilson *et al.* 1996) gives considerably more detailed information on the diet of the selected farmland species and has been independently submitted to the DoE as a separate report.

3.1 Introduction

To understand whether pesticides have indirect effects on bird populations and are implicated in the widespread declines described in Chapter 2, we first need to know which food taxa represent important components of the diet of which bird species, and whether particular food taxa are important across whole goups of similar species. The purpose of this section is to provide this information by review and synthesis of published diet information for the selected British bird species considered to be characteristic of lowland agricultural habitats (Table 2.1). The results provide a basis for further work to assess whether important food taxa are those whose availability is likely to be susceptible to pesticide use, and whether bird species which rely upon pesticide-susceptible food taxa are characterised by declining population trends. The pressing need for work of this kind was recently emphasised by Burn & Cooke (1995).

A full account of the methods used and approach adopted in carrying out the review of diet is given below, although only a summarised version of the results obtained is included in this section of the Review. Full details are included in Wilson *et al.* (1996).

3.2 Methods

Diet information was collated from published papers and reports summarised in the *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic* (BWP) (Cramp & Simmons 1980, 1983; Cramp 1985, 1988; Cramp & Perrins 1993, 1994a,1994b), the *Zoological Record* (1978-1995), and monographs and reprints in the Alexander Library of the Edward Grey Institute, Oxford. Full details of the sources consulted in addition to BWP are given in Wilson et al. (1996).

Studies were classified according to whether diet information was quantitative or not. Quantitative studies were further classified according to one of four methods of data presentation used by the author(s):

1. Frequency of occurrence (e.g. proportion of individuals found to have taken a given food taxon).

2. Percentage of items (e.g. percentage of all food items identified that were of a given food taxon).

3. Percentage of biomass (e.g. percentage of total mass of food analysed that was of a given food taxon).

4. Percentage of feeding observations (e.g. percentage of total prey/food items taken that were of a given food taxon).

Each food taxon was considered 'present' in the diet of a bird species if it was recorded in any of the studies reviewed, and as 'important' either if it comprised a mean of at least 5% of the diet over all quantitative studies reviewed, or if authors of dietary studies stated that they considered it of dietary importance at some time in the annual cycle. The 5% value was chosen as the quantitative threshold for this distinction as it marked a major discontinuity in the distribution of the percentage of diet comprised by food taxa across all studies.

3.3 The diet of farmland bird species: a descriptive summary

A descriptive summary of the diet of all 42 species is given below. This provides supplementary detail, where available, on feeding behaviour, seasonal variation in diet, and comparisons between adult and nestling diet.

Hobby (Falconidae)

Hobbies are opportunist feeders preying on insects and birds in flight, and exploiting local abundances of any suitable prey (e.g. house martin colonies, communal hirundine roosts). Bats, small mammals and reptiles are occasionally taken. On returning to the breeding grounds, insects generally predominate in the diet until the eggs hatch, after which birds are the main prey items for nestlings. There are no records of hobbies taking plant material.

Red-legged partridge, grey partridge, pheasant, quail (Phasianidae)

Partridges feed by picking seeds and invertebrates from plants and from the ground. Invertebrates are taken only during the breeding season and mainly by chicks. Otherwise, partridges subsist on a variety of cereal grains, weed seeds and green plant material. Pheasants and quail are more versatile and will use their feet to dig for roots and tubers. Pheasants will also fly up into trees and shrubs to take fruit. Pheasant chicks feed mostly on invertebrates and adults also take a wider variety of invertebrates throughout the year, including earthworms, ants and beetles. No published data on the diet of wild quail chicks were found. A fuller account of the diet of the grey partridge is given in Chapter 6.

Stone curlew, lapwing, golden plover (Charadriidae)

The diet of these three species consists mostly of invertebrates which are taken both from the ground surface and vegetation, and by probing in soft substrates. All three species detect prey from some distance and will run to catch it, with stone curlews even jumping and half taking off in order to capture flying prey. The lapwing and golden plover are primarily diurnal feeders, whilst the stone curlew is crepuscular and nocturnal in its feeding activity. Very little information is available on the diet of chicks of these three species, but it is generally considered to be very similar to that of the adults.

Barn owl (Tytonidae)

In Britain, by far the most important food of both adult and nestling barn owls is the short-tailed vole *Microtus agrestis*. The common shrew *Sorex araneus* and the wood mouse *Apodemus sylvaticus* are also widely eaten, along with scarcer species such as harvest mouse *Micromys minutus*. Barn owls take some large invertebrates as minor components of the diet - mainly Orthoptera and large beetles (e.g. Carabidae, Staphylinidae, Scarabeidae, Geotrupidae). There is no plant component in the diet.

Little owl (Strigidae)

Little owls take a variety of vertebrate (small mammals and birds) and invertebrate prey. Nestlings are fed a higher proportion of the invertebrate components of the diet (especially earthworms, Orthoptera and beetles, e.g. Carabidae and Geotrupidae) than is taken by adults. In terms of number of prey items taken, invertebrates may comprise in excess of 90% of the diet, but vertebrate

prey usually represents by far the majority by weight. Small quantities of plant material are taken by little owls throughout the year, including maize *Zea*, and a variety of berries and other small fleshy fruits.

Stock dove, woodpigeon, collared dove dove, turtle dove (Columbidae)

These four pigeon species take a variety of plant material, including grain, weed seeds, fruit and green leaves or stems. Invertebrates form a relatively minor component of the diet in all seasons. Most food is taken by pecking from vegetation and the ground, although woodpigeons are more agile than the other species and will clamber around in bushes and trees to obtain buds, leaves and fruit. Other than crop milk, nestling doves and pigeons are generally fed a very similar diet to that available to adults at the same time of year, with the exception of the larger items (e.g. large fruits). Collared doves are visitors to seed food provided in gardens in winter. Stock doves and turtle doves rely much more on the seeds of arable weeds than do the other two species, especially in the case of the turtle dove which shows very little exploitation of cereal, brassica and legume crops and relies almost entirely on the seeds of arable weeds and non-crop grasses. The turtle dove is the only species in this review for which the seeds of fumitories (Fumariaceae) are an important component of the diet.

Skylark (Alaudidae)

The skylark feeds primarily on invertebrates during the breeding season and dependent young are fed almost entirely on invertebrates. Outside the breeding season, skylarks are herbivorous and take a wide range of plant material including grain, weed seeds and fresh shoots of growing wild plants and crops such as cereals and sugar beet. Food is taken by pecking directly at the ground surface or low vegetation, but skylarks will occasionally dig with their bills in loose soil, and frequently search visually in cracks and crevices in dry soil.

Swallow, house martin, sand martin (Hirundinidae)

These three species feed almost exclusively on flying or airborne arthropods caught on the wing and nestling diet is very similar to that of the adults. There is no recorded plant component in the diet of these three hirundines.

Meadow pipit, pied wagtail, yellow wagtail (Motacillidae)

These three species comprise a largely invertebrate-feeding group, taking a very wide range of soft and hard-bodied invertebrates from the ground surface, vegetation, and in the case of wagtails, in the air. Nestlings are fed entirely on the same invertebrates that comprise adult foods. Meadow pipits have been recorded taking seeds, but plant material has not been recorded in the diet of either pied or yellow wagtails.

Blackbird, song thrush, mistle thrush, robin (Turdidae)

Thrushes and chats are omnivorous species which take a wide variety of invertebrates, seeds and fruit, both on the ground and in trees and bushes. During the breeding season invertebrates predominate in the diet of both adults and nestlings, although some fruit may also be fed to nestlings. Robins are frequent visitors to seed foods provided in gardens in winter.

Dunnock (Prunellidae)

The dunnock is a primarily insectivorous species, although a significant proportion of the winter diet comprises seeds. It specialises in very small invertebrate prey found on the ground surface, often amongst loose soil or leaf litter and in herbaceous vegetation and bushes. Nestlings are fed much the same invertebrate diet as is taken by adults.

Wren (Troglodytidae)

Wrens are primarily insectivores, gleaning prey from vegetation surfaces, leaf litter and crevices in bark, rocks or walls, usually within two metres of the ground. Wrens take very little plant material in their diet although some fruits have been recorded.

Spotted flycatcher (Muscicapidae)

Spotted flycatchers feed mostly on invertebrates which may be taken on the wing in 'fly-catching' sallies, gleaned from vegetation or collected on the ground. Some fruit is also taken, especially in autumn. Nestling diet is somewhat different to that of adults with flies, beetles, aphids and caterpillars predominating, but fewer Hymenoptera provided. There is some evidence that when particular prey are unusually abundant (e.g. caterpillar infestations), these may quickly become the primary food of nestlings. Plant material is scarce in the diet of spotted flycatchers.

Red-backed shrike (Laniidae)

Shrikes' sharp, hooked bills allow them to take a variety of large invertebrate and small vertebrate prey. These are hunted on the ground or in low vegetation using a perch-wait-and-strike technique from bushes, fences or other vantage points, although shrikes will feed on the ground in inclement conditions. Large flying insects may be seen at a distance and either chased or caught in a gliding sally from the hunting perch. Most prey are brought back to a perch for consumption, or may be impaled on thorns of a bush used as a 'larder'. Plant material is of little significance in the diet of red-backed shrikes.

Starling (Sturnidae)

Starlings are primarily invertebrate feeders and feed their nestlings almost exclusively on invertebrates taken mostly by probing the soil for soft-bodied prey such as earthworms, leatherjackets and other arthropod larvae, but also direct from the ground surface, vegetation and even by hawking for flying insects. A variety of grain, weed-seed and fruit may be taken outside the breeding season, especially by young birds and when invertebrate food is less easily available. Overall, starlings take a huge range of animal and plant foods and are highly responsive to annual, seasonal and daily variations in the availability of alternative food sources. As such opportunistic feeders, starlings will take advantage of most waste food material provided by humans, although, as noted by Feare (1994) modifications to farm buildings have progressively denied them access to animal feed.

House sparrow, tree sparrow (Passeridae)

Sparrows are predominantly granivorous birds with plant material making up 85-90% of total diet over the whole year, but with invertebrate prey comprising up to 30% of the diet during the breeding season, especially when provisioning their young. Newly-hatched chicks are fed mostly on invertebrates, but the proportion of invertebrate prey fed to nestlings declines as the chicks approach fledging, and the composition of the invertebrate foods shifts from smaller, soft-bodied items (e.g. aphids) to larger prey (e.g. weevils, caterpillars, and grasshoppers). Most food is taken on the ground or by removing seeds and invertebrates from herbaceous plants, although sparrows will perch on ripening cereals to remove grain, and clamber around in foliage of bushes and trees in order to obtain invertebrates. House sparrows readily visit seed-foods provided by humans and may flock in large numbers at grain stores and stock feeding stations. In Britain tree sparrows are much scarcer visitors to such food sources and rarely visit gardens.

Chaffinch, brambling, linnet, greenfinch, goldfinch, bullfinch (Fringillidae)

Finches are primarily granivorous species. All take some invertebrate food during the breeding season and when feeding nestlings, but the importance of this component of the diet varies greatly between the fringilline finches (chaffinch, brambling), which switch to an invertebrate diet during

the breeding season and feed their nestlings on invertebrates, and the cardueline finches (linnet, greenfinch, goldfinch) and bullfinch amongst which a seed diet predominates even during nestling provisioning (Newton 1967). Linnets probably take fewer invertebrates than any other Western Palearctic finch except crossbills *Loxia spp.* and twite *C. flavirostris.* Bullfinches also take considerable quantities of buds and shoots in the spring and may be a serious pest in orchards, especially of plums and cherries, pears, gooseberries and currants, and apples. Finches vary considerably in their feeding methods. Chaffinches and bramblings forage on the ground for seeds, rarely taking them direct from plants, and glean invertebrates from the foliage of shrubs and trees. Greenfinches take seed from the ground and also perch in bushes and trees to take seed from fleshy-fruited species. Goldfinches prefer to perch on the flowers or seed-heads of herbaceous plants to extract seed directly, rather than foraging on the ground, and will also feed in trees, usually to take seeds of pine *Pinus* or alder *Alnus.* Linnets feed on the ground or in low bushes and herbaceous plants to take seed both directly from plants and from the ground, but rarely feed in trees. Bullfinches feed almost entirely in trees and shrubs and very rarely on the ground.

Yellowhammer, cirl bunting, reed bunting, corn bunting (Emberizidae)

Buntings are granivorous outside the breeding season, but switch partially to an invertebrate diet during the breeding season and feed their nestlings almost entirely on invertebrates. All four species feed mostly on the ground, but will sometimes forage in low bushes, especially when gleaning invertebrates during the breeding season.

3.4 The diet of farmland bird species: a taxonomic summary.

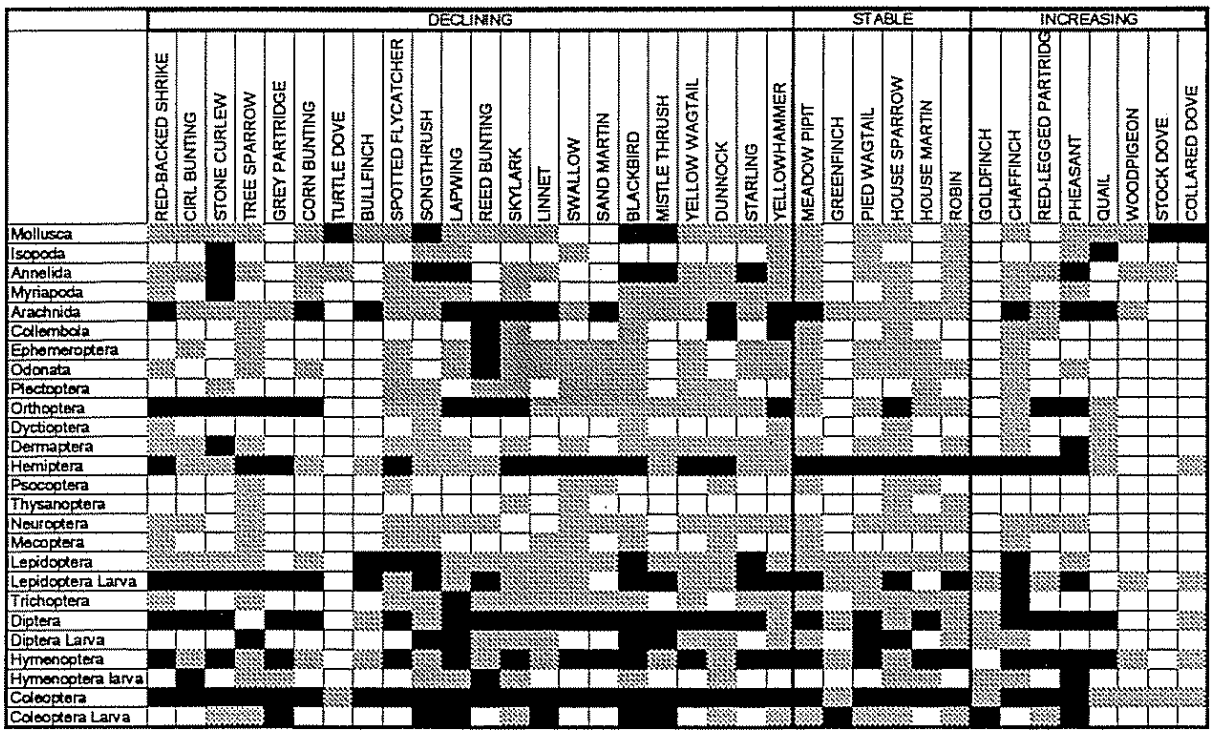
Data were analysed at broad taxonomic levels. Plant foods were classified to the level of families, and animal foods were treated at the phylum/class level, with the exception of insects, where classification was at the order level. Wilson *et al.* (1996) summarise arthropod foods in greater taxonomic detail (family level) for the arthropod orders Coleoptera, Diptera, Hymenoptera, Hemiptera, Orthoptera, and Class Arachnida. Plant food are also summarised in greater taxonomic detail (genera) for the plant families Gramineae, Polygonaceae, Caryophyllaceae, Chenopodiaceae, Compositae, Rosaceae, Cruciferae and Leguminosae in the same report.

The distribution of food taxa across 36 of the 42 bird species is shown in Tables 3.1 & 3.2. The three birds of prey considered in this review (hobby, barn owl and little owl) are excluded from these tables because of the considerable vertebrate component in their diet. Bird species are presented in the order of the extent of their population changes between 1969 & 1994 (see Table 2.1) with the biggest decline on the left and the biggest increase on the right. Where available CBC farmland index change data were used in preference to CBC all habitats data and range change data only used when both the former were not available. Species have been divided into three groups; *declining* (population change > -10%, *stable* (population change -10% ><+10%) and *increasing* (>+10%).

The following system is used in each table:

Cell empty:	not known to be taken as food.
Cell hatched:	present in diet, but not rated (quantitatively or descriptively) as an important dietary component. Further data may show that the food taxon is of quantitative importance in some areas, or that its importance is not quantitative, but limited to a particular period or to a metabolite required only in small quantities.
Cell black:	present in diet and shown either quantitatively or descriptively to be an important dietary component.

Table 3.1. Presence in diet of invertebrate taxa. Bird species arranged in order of population change.



In Tables 3.1 & 3.2 any differences in the diet of declining and increasing species will show up as a gradient in shading from left to right or right to left for a given dietary item. Tables 3.4a and 3.4b show those food taxa which appear to be of widespread importance in the diet of farmland bird communities. Taken together these taxa represent those whose abundance may be of greatest significance as indicators of the availability of food resources for breeding and wintering birds.

For each of the dietary components where there was an apparent difference in the diet of declining and increasing species a Fisher's Exact Probability Test was performed. The proportion of bird species for which the item was important was compared between declining species (n=22 species of birds for which invertebrates were important and 19 species of birds for plant items) and increasing species (n = 8 species of bird for which both invertebrates and plants were important). The proportion of species which had each item recorded in the diet was then compared between the two groups. Significant results are shown in Table 3.3. Note that these results should be treated with caution since no attempt has been made to make a correction for multiple tests. In addition it could be argued that the data concerning diet are not truly independent as a bird foraging in one habitat (e.g. cereal margins) is likely to take a range of available prey from that habitat.

Table 3.2 Presence in diet of plant taxa. Bird species arranged in order of population change.

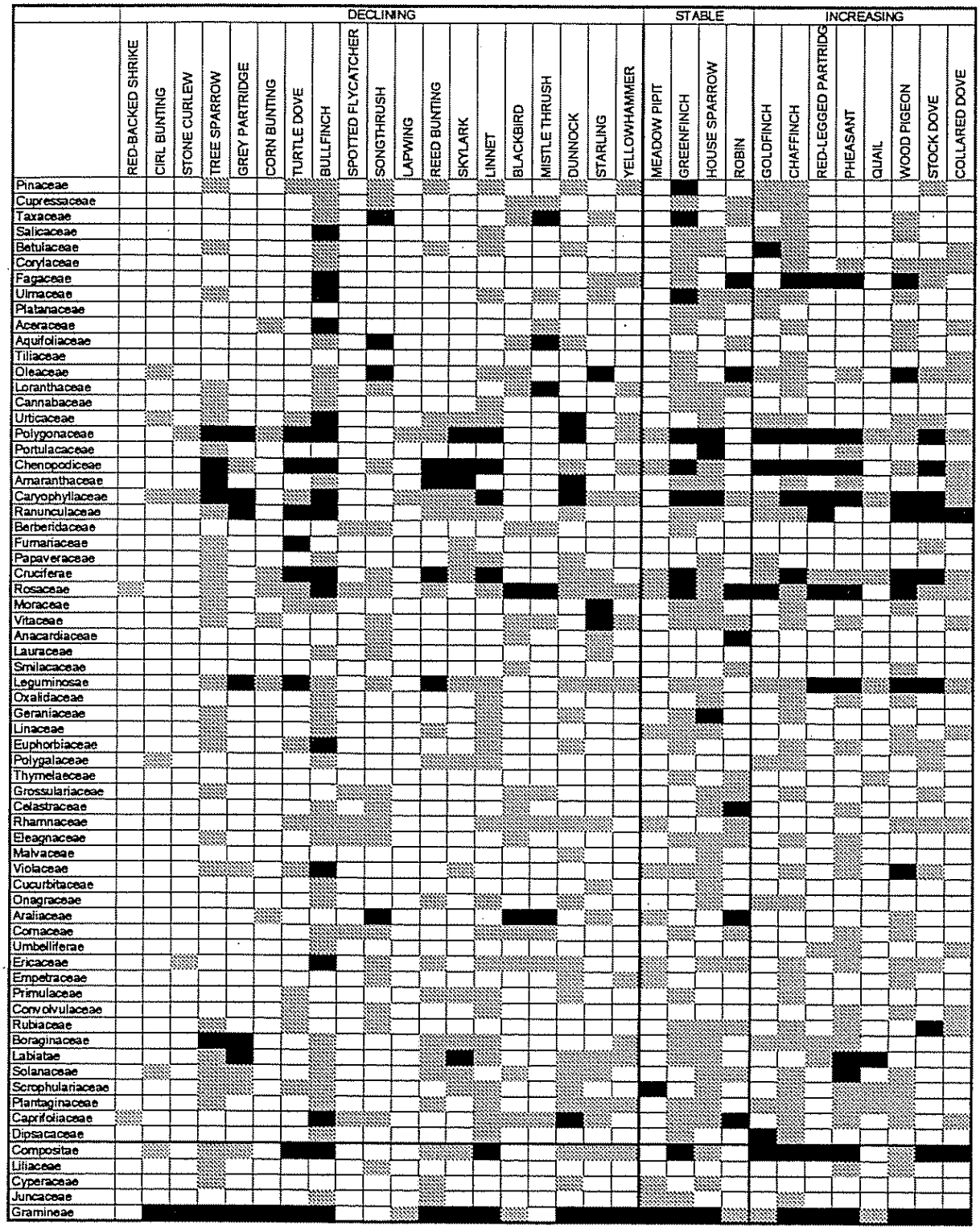


Table 3.3 Analysis of diet review data.

Comparison of dietary components of species which have declined and those which have increased since 1969. The table shows which group had a significantly (at the 5% level) higher proportion of species for which a dietary component was IMPORTANT, *italics,* and which had a higher proportion of species which had that component been simply RECORDED in the diet. For example, Coleoptera was an important component in the diet of a significantly higher proportion of declining than increasing farmland species. Components shown in brackets are significant only on a one-tailed test. (See Tables 3.4a & 3.4b for some more common names of dietary components).

Key dietary components of declining farmland bird species	**Key dietary components of increasing farmland bird species**
(Orthoptera)	
Lepidoptera	
Coleoptera	
	(Salicaceae)
	Corylaceae
	Fagaceae, Fagaceae
	Plantaginaceae
	Tiliaceae
	Thymelaceae
	Rubiaceae
	Compositae

3.5 Discussion

Although able to produc only a very broad and undetailed overview, the review by Wilson *et al.* (1996) does make it possible to identify four very broad categories of animal and plant food taxa. Those that are:

a) of general quantitative importance in the diet of a wide range of farmland bird species, (Table 3.4a & 3.4b in this Review);
b) of particular importance to species currently experiencing population declines in farmland habitats, (Table 3.3 above in this Review);
c) of importance to only a limited range of species, (Table 36 in Wilson *et al.* 1996);
d) taken by a wide range of species, even though not usually being of quantitative importance, (Tables 3.1 & 3.2 above in this Review);
e) clearly avoided by most bird species despite being abundant in farmland habitats.

There are three invertebrate groups which, as dietary components, show some evidence of association with declining bird species (category b). These are Coleoptera (beetles and especially ground beetles), Orthoptera (grasshoppers, bush-crickets and crickets), and Lepidoptera (mainly larval butterflies and moths). It is noteworthy that for each of these groups there is evidence that agricultural intensification has reduced their abundance and diversity in recent decades (Rands & Sotherton 1986; van Wingerden *et al.* 1992; Brooks *et al.* 1995). There are also several plant taxa found in the diet of predominantly increasing species. These include many shrub and tree species including Salicaceae (willows), Corylaceae (hazel), Fagaceae (beech & oak), Tiliaceae (lime), and Thymelaeceae (spurge laurel). Other foods associated with increasing species include Plantaginaceae (plantains), Rubiaceae (bedstraws) and Compositae. There are no plant taxa which are generally associated only with declining birds species.

Table 3.3 a. Invertebrate taxa found to be important components of the diet of a wide range (>9) of the bird species considered. This Table also shows percentage of declining and non-declining species in which each food taxon was considered to be important in the diet (omitting hobby, barn owl and little owl, and four species which are either maintained by releases - red-legged partridge, pheasant - or do not breed on lowland farmland in Britain - golden plover, brambling). See Table 2.3 for the full list of declining and non-declining species.

Invertebrate taxon	Common name	Number of bird spp. for which important in diet (% of declining species / % of non-declining species)	Number of bird species for which taxon was present in diet	Types of birds for which taxon is important
Arachnida		16 (40/40)	19	Invertebrate-feeders, and as nestling food for granivorous species
Araneae	Spiders	14 (40/30)	21	As above
Coleoptera	Beetles	34 (96/60)	5	Most species
Carabidae	Ground beetles	10 (28/10)	21	Larger invertebrate feeders
Curculionidae	Weevils	23 (56/50)	13	As for Arachnida
Orthoptera	Grasshoppers crickets & bush-crickets	13 (44/0)	18	Mainly larger invertebrate-feeders, plus buntings and sparrows
Diptera	Flies	30 (76/60)	6	Most species
Tipulidae	Crane-flies and leather-jackets	12 (36/20)	15	Variety of invertebrate feeders, and nestling food for some granivorous passerines
Hemiptera	Bugs	22 (56/60)	14	Most invertebrate feeders, and important nestling food for Phasianidae and some granivorous passerines
Aphididae	Aphids	14 (32/40)	13	Variety of invertebrate feeders, and important food for nestlings of Phasianidae and finches
Hymenoptera	Bees, wasps sawflies	25 (60/60)	12	As for Hemiptera. Larvae of sawflies important for partridge chicks
Formicidae	Ants	14 (24/50)	19	Important nestling food for Phasianidae, and taken by wide variety of invertebrate-feeders, including Charadriidae
Lepidoptera	Butterflies moths & caterpillars	21 (64/30)	15	Adults and larvae taken by most invertebrate feeders. Larvae important nestling food for most granivorous species

Table 3.3 b. Plant taxa found to be important components of the diet of a wide range (>7) of the bird species considered. This Table also shows percentage of declining and non-declining species in which each food taxon was considered to be important in the diet (omitting hobby, barn owl and little owl, and four species which are either maintained by releases - red-legged partridge, pheasant - or do not breed on lowland farmland in Britain - golden plover, brambling). See Table 2.3 for the full list of declining and non-declining species.

Plant taxon	Common name	Number of bird spp. for which important in diet (% of declining species / % of non-declining species)	Number of bird species for which taxon was present in diet	Types of birds for which taxon is important
Chenopodiaceae	Goosefoots & oraches	12 (28/30)	9	Most granivores, but reed bunting the only bunting
Chenopodium	Goosefoots e.g. fat-hen	9 (24/20)	8	Variety of granivorous passerines, plus pheasant, turtle dove and stock dove
Rosaceae	Rose family	9 (16/30)	18	Cardueline finches, thrushes, wood pigeon, red-legged partridge pheasant
Cruciferae	Cabbage family	8 (16/40)	14	Pigeons, cardueline finches, chaffinch and reed bunting
Caryophyllaceae	Pink family	13 (28/40)	12	as for Chenopodiaceae
Stellaria	Chickweeds	12 (24/40)	8	Phasianidae, pigeons and finches
Compositae	Daisy family	10 (16/40)	11	Phasianidae, pigeons and cardueline finches
Polygonaceae	Bistorts, docks & sorrels	14 (36/30)	11	Most granivorous species, with the exception of buntings
Polygonum	Bistorts, e.g. knotgrass	12 (28/30)	9	Phasianidae, stock dove, turtle dove, skylark, sparrows, chaffinch, greenfinch and linnet
Gramineae	Grasses and cultivated cereals	24 (60/50)	5	Virtually all granivores plus stone curlew, golden plover, starling, meadow pipit and dunnock
Triticum, Hordeum Avena	Wheat, barley oats	17 (28/50)	5	Phasianidae, pigeons, skylark, starling, sparrows, linnet, greenfinch, chaffinch and all buntings except reed bunting

Plant and invertebrate taxa that fall into categories (d) and (e) are numerous. However, some examples are worth emphasising. Amongst the invertebrates, harvestmen (Opiliones), various beetles (e.g. Tenebrionidae, Hydrophilidae, Cantharidae, Byrrhidae, Cerambycidae, Silphidae), flies (e.g. Culicidae, Empididae, Tachinidae, Calliphoridae), bugs (e.g. Cicadellidae, Cicadidae), parasitic wasps (e.g. Braconidae), centipedes (Myriapoda), lacewings (Neuroptera) and a number of groups associated with aquatic habitats (e.g. mayflies (Ephemeroptera), stoneflies (Plecoptera), caddis-flies (Trichoptera)) are taken by a great variety of bird species but are recorded as important in the diet of few or none. Amongst plant foods, fleshy fruits and seeds of roses, rowans, whitebeams, blackthorn (Rosaceae), mistletoe (Loranthaceae), grape (Vitaceae), dogwoods (Cornaceae), buckthorns (Rhamnaceae, Eleagnaceae), bilberry (Ericaceae), woody nightshade (Solanaceae), oraches (Chenopodiaceae), spurges (Euphorbiaceae), and speedwells (Scrophulariaceae) all fall into the same categories (d & e).

It is amongst plants where taxa that are largely avoided by feeding birds are most noticeable. Thus, of families which are well represented among the wild flora of lowland farmland, the seeds of fumitories (Fumariaceae), poppies (Papaveraceae), cranesbills (Geraniaceae), St John's worts (Guttiferae), willowherbs (Onagraceae), umbellifers (Umbelliferae), bindweeds (Convolvulaceae), and bedstraws and cleavers (Rubiaceae) are all relatively little exploited by granivorous species. Even so, the preference of turtle doves for the seeds of fumitory re-emphasises the fact that however well we may identify the range of taxa that are of general importance as food sources for farmland bird communities, there remain individual species preferences which must be taken into account. Of the major invertebrate taxa, only those represented by parasitic species (e.g. lice - Mallophaga, Anoplura) or other very small animals (e.g. most apterygotes and thrips - Thysanoptera) are infrequently recorded in bird diet, presumably because their small size makes them of little nutritional value, as well as being difficult to find.

Any general review of the diet of birds of lowland farmland, such as the one presented above, must be interpreted with caution. Lack of information on relative abundances of available food taxa, seasonal and geographical biases, difficulty in identifying certain food items, and biases in recorded diet composition created by different methods of diet analysis (e.g. faecal sample analysis versus stomach content analysis) all may distort any assessment of the dietary range and composition of any one species over the entire annual cycle. Detailed studies of individual species of birds will undoubtedly reveal the importance of other invertebrate and plant taxa, including some which do appear to be important in the above review.

Detailed studies of diet throughout the year, in contrasting agricultural landscapes, and collation of data from different methods of diet measurement would be desirable for most of the species in this review. Such work is, however, very labour-intensive and relevant data are likely to accumulate only slowly. It would also be desirable to understand diet composition in relation to the range of foods available to birds. This would allow us to move from simple statements about which potential foods are present and which are quantitatively important in the diet, to an understanding of which food taxa are preferentially selected and which avoided. To achieve this level of understanding for all species is a daunting prospect. Measuring the abundance of different food taxa requires a variety of different sampling methods. Even within one sampling method (e.g. vacuum sampling or pitfall trapping of invertebrates), biases in sampling efficiency may be created by variation in habitat (e.g. Duffey 1980; Topping & Sunderland 1992). Moreover, many of the food taxa referred to in this review include many ecologically diverse species whose niche differences will greatly affect their likely availability as prey items for foraging birds. The contrast between diurnally and nocturnally active carabid beetles provides a simple example.

Even on those occasions when diet composition has been set in the context of food availability within the study area (e.g. Newton 1967), it may not be clear why particular food taxa are preferred and others avoided. Studies by Gluck (1985) and Whitehead (1994) of goldfinches and starlings respectively provide good examples of the complex trade-offs between nutritional value, handling time, spatial distribution and predation risk that may determine whether particular food types are favoured or avoided. Even good quantitative data on diet composition coupled with a knowledge of patterns of preference for, or avoidance of, particular foods will not provide a complete picture of

the relative importance of different foods. For example, certain foods may be of critical importance, but only in tiny quantities, or over very short time periods. A good example of the former is the requirement of the females of many species for a dietary source of calcium prior to egg-laying. Snails are one example of a prey item rich in calcium which may be important for many bird species at this time (Graveland 1995). It is conceivable that the apparent importance of snails in the diet of otherwise almost exclusively herbivorous doves (Table 3.1) may reflect this need, but are there other food taxa which, although not of quantitative importance in birds' diet, also provide essential sources of calcium or other substances necessary in small amounts? The importance of small, soft-bodied invertebrates (e.g. caterpillars, spiders and aphids) for the young nestlings of many species in this review is one example of the probable time-limited importance of certain food types.

3.5 Conclusions

Although comprehensive quantitative data on the diets of the majority of farmland birds are not available, it is clear that most species have relatively wide and varied diets, which include a range of plant and invertebrate species that live within the cropped area and adjacent habitats that are an integral part of the present lowland farmland landscape. Individual species vary in the extent to which either plants or invertebrates predominate in their diets, but the majority depend on invertebrates at least when they are newly hatched. Although not unexpectedly, bearing in mind the breadth in diet of many species, there are no very obvious gross differences in the diets of the declining and stable or increasing bird species, Lepidoptera, Coleoptera and Orthoptera feature more prominently in the former and shrubby or woodland plants in the latter.

In most groups of similar farmland birds there are both declining and stable or increasing species, but in two all species appear to be in decline. The thrushes, although omnivorous, all feed mainly on invertebrates throughout the breeding season and may be particularly susceptible to shortages of, for example, snails, worms and insect larvae. Likewise whilst buntings are generally granivorous, they switch to feeding invertebrates to their nestlings, especially when very small, and again may be vulnerable to shortage of invertebrates.