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BRITISH BIRDS

Predation by birds on social wasps

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INTRODUCTION

It is well known that bee-eaters (Meropidae) and the Honey Buzzard* prey extensively on stinging Hymenoptera. However, the extent to which other birds feed on stinging insects is poorly known. This paper examines published records of birds feeding on the social wasps of the genus *Vespula* and on the Hornet *Vespa crabro* (Hymenoptera, Vespidae) and draws attention to the various reactions of the birds to their stinging mechanism and toxicity. It is confined mainly to birds of Europe and the USSR feeding on European species of wasps.

The following social wasps occur in Britain and Ireland and over much of Europe: Common Wasp *Vespula vulgaris*, German Wasp *V. germanica*, Red Wasp *V. rufa*, Norwegian Wasp *V. norvegica*, Tree Wasp *V. sylvestris* and Cuckoo Wasp *V. austriaca*.

In the present paper much of the information collected is of incidental observations, recorded as short notes. Although a large amount of work on the relationships between birds and distasteful insects has been carried out, the social wasps have received little attention. Hesse (1916) recorded a list of birds predatory on social wasps, and Charlemagne (1954) commented on the predation by birds on stinging Hymenoptera, but there have since been a number of further records. In North America, McAtee (1932) collected 822 records of Vespoidea being eaten by a total of 140

* Scientific names of birds feeding on wasps are given in the appendix on page 229.

(unnamed) species of birds, and used this, together with other information, in an attempt to demonstrate that protective adaptations in animals are not effective. These suggestions were subsequently criticised by a number of workers (Anon 1934), and Cott (1940) came to the opposite conclusion.

WARNING COLORATION

All social wasps have a striking black and yellow pattern which is generally regarded as an aposematic (warning) coloration, and all females (queens and workers) possess powerful stings. I have suggested (Birkhead 1973a) that the similarity of the colour markings among social wasps prevents potential predators from distinguishing the species, so that the group probably forms a series of Mullerian mimics. If this is so, a predator may learn to avoid all the species as a result of one or a few encounters with individuals of any species. In certain groups of insects, such as danaid butterflies (Danaidae), the whole creature may be distasteful, but other insects, such as the social wasps and bees (Apoidea), may be quite palatable except for the stinging mechanism. Therefore, if a particular predator can overcome the sting either by removing or destroying it, or by being sufficiently protected not to be stung, or through possessing some degree of immunity to venom, the aposematic coloration would cease to operate protectively for the insect in question.

PALATABILITY AND WASPS AS AVIAN PREY

There is good evidence that at least some birds find social wasps palatable; in fact, a few habitually feed on stinging Hymenoptera and have developed methods of avoiding the insects' stings.

1. Bee-eaters. All species take stinging Hymenoptera, though as their name suggests these are usually bees *Apis spp.* The European Bee-eater also takes social wasps (Witherby *et al.* 1938-41, Matoušek 1951, Hachler 1958, Maran 1958, Fintha 1968, Herrera and Ramírez 1974). Charlemagne (1954) recorded that during August near Kiev, USSR, the stomachs of Bee-eaters contained Hornets and wasps exclusively. Bee-eaters have a highly stereotyped and efficient method of dealing with venomous insects, which Fry (1969) has described in detail. Stinging insects are de-venomed by a sequence of beating and rubbing the prey rapidly against the perch. This treatment discharges the venom on to the perch and apparently renders the insect harmless and edible. Bee-eaters are able to recognise drone bees and non-stinging insects, which they do not subject to such severe treatment as venomous forms (Fry 1969, 1972).

2. Shrikes (Laniidae). Three species have been recorded feeding on social wasps: Great Grey (Witherby *et al.* 1938-41, Boháč 1964, Cade 1967), Lesser Grey (Hesse 1916, Charlemagne 1954) and Red-backed (Owen 1929, Necas 1942, Charlemagne 1954). The food and hunting techniques of the Great Grey Shrike in North America have been examined by Cade (1967). He found that this species took large numbers of social wasps and that these and other insects were always caught in the beak (while bird or mammal prey was sometimes taken in the feet). Cade also suggested that after locating a wasps' nest this species may systematically take all the adult (flying) members.

Gwinner (1961) made a detailed study of sting removal from Hymenoptera by Red-backed Shrikes. He found that they destroyed the stinging apparatus by squeezing the tip of the abdomen and rubbing it against the perch. Gwinner stated that this pattern of behaviour was apparently elicited by the specific elasticity of the insect's thorax, though the size and movements of the prey animal were also important. In addition, the moving sting was found to intensify the bird's reaction. I can find no record of Great Grey or Lesser Grey Shrikes preparing hymenopterid prey in this manner, though it seems highly probable that they do so.

3. Honey Buzzard. Despite its name, the main foods of the Honey Buzzard are the immature and mature stages of social wasps (Thorburn 1925, Witherby *et al.* 1938-41, N. N. Somov in Charlemagne 1954). Hagen and Bakke (1958) found that in southern Norway the Common Wasp was the main prey species, and most other authors refer to Honey Buzzards taking the nests of ground-nesting social wasps, digging them out with their feet, but Voous (1960) also mentioned nests of arboreal wasps—Norwegian and Tree Wasps—being raided. According to J. G. Millais (in Thorburn 1925), Honey Buzzards follow wasps to their nests and then excavate and consume the contents. This author also recorded that birds appeared indifferent to the attacks of the wasps, but Trap-Lind (1962) observed a Honey Buzzard attacking a wasps' nest and, on examining the remains of the nest later, he found many decapitated wasps. Wood (no date) suggested that Honey Buzzards are vulnerable only at the base of the beak and around the eyes but, as Willis (1972) pointed out and my own examination of museum specimens confirms, the feathers around the head are small, stiff and close fitting, presumably forming an efficient barrier against the stings.

In addition to those commonly known to take adult wasps, many other species of birds have been recorded eating these insects (see appendix). Some of these are of particular interest.

Fincher (1951) described how a first-year Great Tit took a wasp

(probably either Common or Norwegian), held it with its foot and pecked at it. The first beakful was not eaten, but he could not determine whether this was the sting; succeeding beakfuls were eaten. Tutman (1949) recorded Great Tits removing the stings of dead Honeybees *A. mellifera*. C. Elmhirst (in Knubley 1889), Hesse (1916), Charlemagne (1954) and S. M. Pospelov (in Dementiev and Gladkov 1966-68) recorded Great Tits eating wasps, and there are also references to bees found in the stomachs of Great Tits (Newman 1863, Norgate 1881, Pospelov *loc. cit.*), indicating that these birds are capable of coping with venomous Hymenoptera. These observations contrast with those made by three independent observers of Blue Tits *Parus caeruleus*, which avoided social wasps. Rankin (1950) and Powne (1951) both noted that, when Blue Tits approached a bone upon which wasps were already feeding, they appeared to be wary and did not alight on the bone. Rogers (1951) also observed wasps driving Blue Tits off ripening fruit. Although these observations differ from those on Great Tits, the latter are not adequate to suggest that this would not be a normal response from them also, in similar situations.

Some observations of birds feeding on Honeybees are enlightening. Tutman (1949) recorded Great Tits entering beehives on very cold days to feed on dead bees, when the live occupants were in a torpid condition. He also noted that at other times Great Tits were apparently 'afraid' of live bees. Manley (1948) recorded Great Tits, Blue Tits and sparrows (House Sparrows *Passer domesticus*?) taking bees in the vicinity of hives. These observations raise the possibility that birds may take advantage of torpid insects. Under certain weather conditions, particularly on damp, misty days, I have observed torpid social wasps and bumblebees on flower heads. Stinging insects in a torpid condition would be relatively easy prey for birds.

There are several records of crows (Corvidae) eating social wasps. There are references to Rooks (Anon 1916, Marie 1923, Holyoak 1972) and Magpies (Csiki 1919, Goodwin 1952, Bährmann 1968) with wasp remains in their stomachs. Jays have been recorded feeding on a variety of wasp species, including Hornet (Stachanoff 1928) and Red Wasp (Inozemtsev 1965), and may regularly do so (Goodwin 1952). Owen (1956) found that wasps were fed to nestling Jays, and Campbell (1936) and Keve and Sterbetz (1968), during their analyses of stomach contents of adult Jays, found remains of social wasps. Charlemagne (1954) recorded that in the autumn, when wasps emerge *en masse* in the USSR, the stomach contents of 47 Jays contained 70% wasps. Goodwin (1952) found that his captive Jays readily ate wasps, and described how the birds dealt with them. The wasp was bitten hard as the bird seized it and thus disabled it, after which the Jay directed several pecks at the posterior

end of the abdomen before eating the insect. It is of interest that Goodwin also suggested that this behaviour is innate in Jays, since two naïve birds treated wasps in a way similar to that seen in experienced birds.

WASP LARVAE AND PUPAE AS BIRD FOOD

Gilbert White (1789) recorded that his bantam fowls were particularly fond of the 'young wasps in their maggot state' when a wasps' nest was provided for them. There is evidence to suggest that other bird species find the immature stages an attractive food. J. F. Naumann (in Dresser 1881) stated that Green Woodpeckers sometimes raid wasps' nests, and there is also a record of a Grey Heron feeding on wasp larvae (Witherby *et al.* 1938-41). R. L. Winter (verbally) has observed a Jackdaw tearing at the nest of a ground-nesting wasp and noted that the bird did not appear to be bothered by the adult wasps which were flying around the damaged nest. A group of eight Magpies was seen tearing at a nest (Mather 1971), and I watched nine Magpies gorging themselves on the combs and their contents of two nests of Common Wasps, which had been placed on the lawn of a garden (Birkhead 1973b). Although the latter situation was artificial, the behaviour demonstrated that Magpies find this food attractive. It would be of interest to know whether Magpies regularly attack wasps' nests.

While some birds may be capable of killing and eating isolated wasps, a collection of larvae and pupae poses a particular problem, since the predator is likely to encounter large numbers of aggressive adult wasps when attempting to raid a nest. The Honey Buzzard is apparently sufficiently protected to do this, and other birds such as Magpies and Jackdaws may also be. Some birds may also take advantage of wasps' nests which have already been broken into by Badgers *Meles meles* or by man.

TOXICITY OF WASPS

Leipelt (1963) observed the reactions of captive Redstarts and Pied Flycatchers to social wasps and their venom. He provided mealworms covered in venom, which the birds clearly found distasteful, reacting by head-shaking and bill-wiping. Apparently the birds' buccal mucosa was sensitive to the venom. During some experiments in which he presented live wasps, two Redstarts were stung in feeding attempts. In the first case the bird fluttered wildly about its cage, but Leipelt removed the sting from its tongue and it soon settled down. In the second case the bird was stung near the base of the bill, and reacted by fluttering excitedly; this was followed by a six-hour period of apathy, but after seven hours Leipelt considered

the bird to have recovered. Although the effect of the sting was not fatal, if a wild bird were stung during the afternoon and were unable to feed for six hours it would probably not have sufficient food reserves to survive the night. In addition, a bird which has been stung may be more vulnerable to predation. It is interesting that Leipelt also recorded that some naïve birds captured wasps, and although they were not stung they showed distress symptoms as a result of the venom coming into contact with the buccal mucosa.

In an experiment recorded by Cott (1940, page 293), it was observed that Coots *Fulica atra* ignored wasps floating on the water. However, on one occasion wasps were taken by both a Coot and a Mallard *Anas platyrhynchos* when a mixed group of these species was excitedly fighting over floating food. The insects were immediately rejected and head-shaking and bill-wiping followed. These are the only examples I could find of birds apparently stung by wasps. There are few records of birds apparently stung by other Hymenoptera, but Fry (1969) observed an immature Red-throated Bee-eater *Merops bullocki* exhibiting distress symptoms after eating its first few bees, and suggested that it had been stung.

A number of authors have recorded that birds are able to distinguish between stinging and non-stinging insects (Lacey 1910, Grant 1945); and Swifts *Apus apus* (Lack 1956) and Red-throated Bee-eaters (Fry 1969) can recognise male (non-stinging) bees from female (stinging) castes. Leipelt (1963) noted that his captive Redstarts and Pied Flycatchers could distinguish male wasps. However, it is not known how birds are able to recognise stinging insects. In several families of Vespoidea the male caste has developed a pseudo-sting (Evans and Eberhard 1970); this is particularly noticeable in the potter and mason wasps (Eumenidae) but less obvious in the social wasps. It seems probable that, by mimicking the females' sting, the pseudo-sting may confer some additional protection to male wasps.

The principal components of venom of vespid wasps are a protein which produces allergic reactions in man, an acetylcholine-like substance, histamine, serotonin and kinin, and the amount of venom injected in a single sting varies from 0.05 to 0.3 ml (Spradbery 1973). The variation in human reaction to wasp stings is well known and birds may be equally variable in their reactions. Clearly, however, because of their smaller size birds may be more sensitive to sting effects unless they possess some immunity.

Phisalix (1935) is apparently the only worker to have examined the effects of insect stings on birds. He found that 0.6 mg of *Apis* venom per 100 gm of body weight proved fatal to sparrows. Fry (1969) calculated that on this basis a single sting would prove fatal to the Red-throated Bee-eater if it possessed no physiological immunity.

DISCUSSION

Feeding on isolated wasps and raiding nests in order to feed on larvae and pupae require different strategies. In the first situation birds must overcome the mechanical effect of the wasps' stings in the mouth and gut, and the physiological effect of the venom. In the second situation a bird must be sufficiently protected to avoid being stung while attacking a nest.

Birds which regularly feed on isolated wasps, such as bee-eaters and shrikes, have specialised behaviour patterns enabling them to disarm their prey. It is interesting that the Jay shows a similar pattern of preparatory behaviour. In contrast, Honey Buzzards apparently ingest wasps without any preparation, though they have been recorded decapitating them. However, decapitation would not prevent a wasp from stinging once inside the predator's mouth or gut. Apparently there is no record of an examination of the mouth or alimentary canal of the Honey Buzzard to determine whether it shows any adaptations. In view of the large numbers of wasps that Honey Buzzards eat, it seems likely that they possess either morphological adaptations of the mouth and oesophagus or some immunity to venom. On the other hand, bee-eaters' apparent immunity to Hymenoptera venom in general (Fry 1969) may be more of a safeguard, in view of their elaborate preparatory behaviour. It has not been demonstrated whether shrikes possess any immunity.

The small number of bird species that has been recorded raiding nests of social wasps indicates that the insects' defence (see Spradbery 1973) is highly effective. Wasp larvae and pupae are probably an attractive food, but in order to predate a nest successfully a bird must be sufficiently protected to avoid being stung. It is interesting that I have found no records of small birds attacking wasps' nests. The relatively thicker plumage of larger birds may provide protection, though Skutch (1971, pages 270-271) recorded tanagers *Piranga spp* in the tropics and USA attacking wasps' nests. Three of the records of birds feeding on nest contents involve corvids: these are well known to be opportunists, ready to take advantage of any such abundant supplies of food.

In conclusion it may be said that, although a wide range of bird species has been recorded preying on social wasps, only very few regularly do so, indicating that the insects' defence mechanisms, on both an individual and a co-operative basis, are effective.

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SUMMARY

Predation by European and Russian birds on social wasps (Vespidae) is reviewed. At least 37 species have been recorded feeding on social wasps, but only a few do so regularly, namely bee-eaters (Meropidae), shrikes (Laniidae) and the Honey Buzzard *Pernis apivorus*. Jays *Garrulus glandarius* and Great Tits *Parus major* may also take these insects more frequently than is supposed. All species which regularly feed on stinging insects have behavioural or morphological and physiological adaptations, or both. The few records of birds stung by wasps indicate that venom is not necessarily fatal, though birds which have been stung are at a disadvantage.

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Appendix. European and Russian bird species recorded as having eaten social wasps (Vespidae) in adult (A) and larval (L) stages

Hesse (1916) recorded the Common Wasp *Vespula vulgaris*, German Wasp *V. germanica*, Tree Wasp *V. sylvestris*, *V. (polistes) gallica* and Hornet *Vespa crabro* in avian crops, stomachs or pellets, but did not specify which birds had eaten which wasp species. Vaughan (1961) and Dementiev and Gladkov (1966-68) recorded only 'wasps', with neither generic nor specific names

Grey Heron *Ardea cinerea* (A, L)	Vasvari 1948-51, Witherby *et al.* 1938-41
White Stork *Ciconia ciconia* (A)	Hesse 1916
Buzzard *Buteo buteo* (A)	Hesse 1916
Honey Buzzard *Pernis apivorus* (A, L)	Witherby *et al.* 1938-41, Hagen and Bakke 1958
Hobby *Falco subbuteo* (A)	Hesse 1916
Eleonora's Falcon *Falco eleonorae* (A)	Stresemann 1943, Vaughan 1961
Red-footed Falcon *Falco vespertinus* (A)	Charlemagne 1954
Lesser Kestrel *Falco naumanni* (A)	Charlemagne 1954
Partridge *Perdix perdix* (A)	Hesse 1916
Black-winged Pratincole *Glareola nordmanni* (A)	Dementiev and Gladkov 1966-68
Little Owl *Athene noctua* (A)	Hesse 1916
Alpine Swift *Apus melba* (A)	Witherby *et al.* 1938-41
Needle-tailed Swift *Hirundapus caudacutus* (A)	Zolotarev in Dementiev and Gladkov 1966-68
Bee-eater *Merops apiaster* (A)	Hesse 1916, Witherby *et al.* 1938-41, Dementiev and Gladkov 1966-68, Fry 1969
Roller *Coracias garrulus* (A)	Bernáth 1958
Green Woodpecker *Picus viridis* (A, L)	J. F. Naumann in Dresser 1881, Hesse 1916
Great Spotted Woodpecker *Dendrocopos major* (A)	Hesse 1916
Hooded Crow *Corvus corone cornix* (A)	Hesse 1916
Rook *Corvus frugilegus* (A)	Anon 1916, Hesse 1916, Marie 1923, Holyoak 1972
Jackdaw *Corvus monedula* (A, L?)	R. L. Winter verbally
Magpie *Pica pica* (A, L)	Hesse 1916, Goodwin 1952, Mather 1971, Birkhead 1973b
Nutcracker *Nucifraga caryocatactes* (A)	Hesse 1916
Jay *Garrulus glandarius* (A)	Hesse 1916, Campbell 1936, Goodwin 1952, Owen 1956, Dementiev and Gladkov 1966-68
Great Tit *Parus major* (A)	Hesse 1916, Fincher 1951, S. M. Pospelov in Dementiev and Gladkov 1966-68
Blackbird *Turdus merula* (A)	Hesse 1916
Rock Thrush *Monticola saxatilis* (A)	Hesse 1916
Black Wheatear *Oenanthe leucura* (A)	Richardson 1965
Redstart *Phoenicurus phoenicurus* (A)	Leipelt 1963
Blackcap *Sylvia atricapilla* (A)	Witherby *et al.* 1938-41
Garden Warbler *Sylvia borin* (A)	Charlemagne 1954
Whitethroat *Sylvia communis* (A)	Charlemagne 1954
Spotted Flycatcher *Muscicapa striata* (A)	Owen 1914
Pied Flycatcher *Ficedula hypoleuca* (A)	Leipelt 1963
Great Grey Shrike *Lanius excubitor* (A)	Witherby *et al.* 1938-41, Cade 1967, Grönlund *et al.* 1970
Lesser Grey Shrike *Lanius minor* (A)	Hesse 1916
Red-backed Shrike *Lanius collurio* (A)	Cajander 1929, Owen 1929, Witherby *et al.* 1938-41, Gwinner 1961
Starling *Sturnus vulgaris* (A)	Hesse 1916, Szijj 1956-57

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