A REVIEW OF THE ANTING-BEHAVIOUR
OF PASSERINE BIRDS

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(Plates 57-62)

INTRODUCTION

Anting-behaviour may be defined as the stereotyped movements with which birds, in order to get formic acid (or other organic liquids) on to the feathers for some purpose as yet not fully understood, actively apply ants (or objects in place of ants) to certain parts of the plumage, and/or more or less passively allow these insects to crawl on to the plumage.

Bird-watchers in the British Isles have so far lacked a readily available general review of this enigmatic behaviour. The present paper aims to provide detailed descriptions of the special movements involved (with the aid of illustrations) and to discuss the nature of anting critically.

The literature of anting and the basis of the present review.

No attempt will be made to trace fully the earlier history of anting in the literature. Those interested can do no better than read the account of Chisholm (1944), to whom all credit is due for first stimulating widespread interest in this very puzzling phenomenon in his book on Australian bird topics (1934). Before this, there were only scattered references (e.g. Osmaston (1909) who gave the first details of certain features of anting), but, as a direct result of Chisholm's comments, there appeared, in the German periodical Ornithologische Monatsberichte, a series of preliminary notes, initiated by the editor Dr. E. Stresemann (Stresemann, 1935; Stresemann et al., 1935; Adlersparre, 1936; and others). Another contribution at this time came from India (Ali, 1936), after which for some years most interest in anting was shown in North America, mainly through the medium of The Auk. After McAtee (1938) had written the first general review, papers and notes greatly multiplied. The most valuable of these are by Ivor (1941, 1943), based on an unrivalled amount of first-hand information of anting in aviary birds, while other American papers...
which have added appreciably to our knowledge of the subject are those of Nice and ter Pelkwyk (1940), Nice (1943), Brackbill (1948) and Groskin (1950). In recent years, further contributions have appeared in Europe, including major reviews by Wackernagel (1951), van IJzendoorn (1952) and Poulsen (1956a and b). In Britain, the most important papers are those of Goodwin (1953, 1955b, 1956); otherwise, in spite of Chisholm's (1944) review in *The Ibis*, anting-behaviour has received little detailed attention here, most contributions taking the form of short notes in *British Birds*. An interesting summary was included by Rothschild and Clay (1952) in their book on bird-parasites and one of the most recent additions to the anting-literature is an attractive paper by Ivor (1956), illustrated by colour flash-photographs.

As the bibliography shows, the literature on anting is a large one. Out of it all, the works of Ivor, of Goodwin (also 1951, 1952, 1955a) and of Poulsen are of the most value, being based on very close study of numerous species in captivity. My debt to those authors is particularly great in preparing this review. I have also, however, been able to draw on my own experiences of anting. This has been mainly with my captive Pekin Robins (*Leiothrix lutea*) though I have also had the opportunity of watching a further twenty or so species, chiefly while accompanying Derek Goodwin at the London Zoo. Full acknowledgements are made at the end of the paper.

**SOME GENERAL ASPECTS**

True anting seems entirely confined to the Passerines. In 1943, Nice traced records for nearly forty species of thirteen families; in 1952, van IJzendoorn for over sixty species of eighteen families, and in 1956, Poulsen for nearly 110 species of twenty-four families, of which he himself was responsible for no less than over forty new records. The behaviour is most common in the crows (*Corvidae*), starlings (*Sturnidae*), troupials or hang-nests (*Icteridae*), finches (*Fringillidae*), weavers (*Ploceidae*), thrushes (*Turdidae*) and babblers (*Timaliidae*). However, even in these groups the behaviour is not shown by all members, and there are some whole families which apparently never "ant", for example the larks (*Alaudidae*), tits (*Paridae*) and warblers (*Sylviidae*). An annotated list of those British and other European species that have been recorded as anting is given on pages 413-415. Anting has also been reported from the woodpeckers (*Piciformes*), but confirmation is needed of this as no authority, either on anting or on woodpeckers, has recorded the behaviour from this group. The problem will be discussed in more detail later (p. 412). The game-birds (*Galliformes*) are supposed to "ant" too, but Goodwin (1955b) points out that here we have to avoid confusion with mis-interpreted dust-bathing in ant-hills. Poulsen (1956b) confirms this. He gave fifteen individuals of six game-bird species, representing six genera, the opportunity to "ant", but none did
so though all ate the insects. Partridges (*Perdix perdix*) and Quail (*Coturnix coturnix*) were among the species studied.

There are two major types of anting, active-anting and passive-anting, the main differences between the two being that, in the former, the bird normally applies crushed ants directly to certain parts of its plumage with the bill, whereas, in passive-anting, it usually assumes a special posture in order to allow live ants to crawl over it. These variations are not absolute; intermediate behaviour occurs and birds that are passive-anting will perform active-anting movements at the same time. Before describing these activities in detail, the general relationship of birds with ants should first be examined briefly.

In the British avifauna, only two species, the non-Passerine Wryneck (*Jynx torquilla*) and Green Woodpecker (*Picus viridis*), are regular eaters of ants. Probably no Passerine relies on them to any great extent as major items of diet, although many will at least occasionally consume even the workers, will pay special attention to swarms of winged ants and will eagerly eat the pupae ("ant-eggs") if given an opportunity. Here, we are mainly concerned with the worker-ants which produce acid (as also do the less numerous queens, though the male ants are harmless). All the evidence suggests that birds will eat worker-ants only if other, more desirable, food is not readily available. However, we do urgently need further observations on ants as food and these are not easy to make under field-conditions; moreover, work on aviary birds, which usually do not get a fully natural diet and cannot forage normally, may be misleading in this particular case. Theoretically, it might be supposed that worker-ants would be protected to some extent from predation by the formic acid they manufacture internally and secrete. Indeed, the work of Palmgren *et al.* (1937) and of Steiniger (1937) did indicate that workers were avoided by birds because of their distastefulness. Robins (*Erithacus rubecula*), one of the species observed in captivity, approached the ants, showed interest in them but would not touch them. Evidence such as this led Heikentinger (1954) to state that the avoidance of worker-ants is absolute. However, Poulsen has recently found that captive Robins will eat ants readily on occasions, even workers of the large Wood Ant (*Formica rufa*), which shows that the avoidance is only relative.

Birds' reactions to worker-ants vary. For example: some species, such as the Robin, pick them up rapidly and swallow them immediately without nibbling them first and apparently without ever anting with them (Poulsen, 1956b); others, such as the Jay (*Garrulus glandarius*), never eat the workers but do "ant", while many Passerines both consume them and perform anting. Feeding and anting frequently occur together, but this is by no means always so. It must be remembered that observations on birds anting in captivity are done in rather artificial circumstances which might bias one into stressing too greatly the connection
between anting and feeding. In the wild, birds are not often confronted with an upturned ant-colony—nest debris, very edible pupae and males, queens and workers together. Sometimes birds will approach worker-ants specially to "ant" with them, often discarding them afterwards, which suggests that anting is, in fact, independent of feeding. This point is further discussed on pages 416-417.

Worker-ants of several species squirt acid at their foes. The largest British species, the Wood Ant, stands up, brings its abdomen forward between the legs and directs a jet of formic-acid as far as six to twelve inches (Imms, 1947). Normally, birds are well protected by their feathers against this form of attack, which in any case is mainly designed to deal with other insects, not vertebrates. On occasions, however, this acid reaches the area of a bird's eye when it is feeding or anting. The most common reaction to this unpleasantness is the characteristic "shoulder-rubbing" movement (Goodwin, 1955a), the head being flicked down to the shoulder in order to rub the eye against it. This behaviour is not a special movement connected only with anting. Species of many orders which do not "ant" show it when any irritation, such as dust or dirt, affects the eye. Less commonly, birds with acid in the eye may wipe the side of the head on a branch or scratch with the foot. At other times, a bird will leap back, shaking the head and blinking the eye. Birds are less perturbed when squirted on the legs, but Poulsen (1956b) notes that they may shake their legs, jump, and pick off those ants on the tarsi to fling them away.

**DESCRIPTION OF ANTING-BEHAVIOUR**

*Active-anting* (Figs. 1-2, plates 57-61).

The majority of those Passerine species that "ant" do so actively. The movements by which they do so are performed so rapidly that the details are very hard to follow, especially at a distance in the field. Indeed, most field-notes on anting tend to be rather vague, incomplete and, in some cases, inaccurate. This is no reflection on the observers themselves but on the extreme difficulty of noting down exact details, especially for those not familiar with anting-behaviour. Thanks now to the patient observations of several ornithologists on captive birds, and to the flash-photographs in Ivor (1956), these superficially very complex movements are revealed as relatively simple and stereotyped. Most Passerines adopt a characteristic posture as they apply ants along the underside of the wing (on the outer primaries mainly) and also, though perhaps less frequently, under the tail (again chiefly on the outer rectrices). Some crows and Purple Grackle (*Quiscalus quiscula*: Family Icteridae) excepted, it is extremely doubtful whether any other birds rub ants on additional parts of the body, such as the contour-feathers, as some field-observations have indicated but no anting authority confirmed.
Ivor (1956), who has observed anting on thousands of occasions (sometimes even on his hand) and who has studied 250 flash-photographs (some of which are published here), never once saw ants being applied to the body. He tells also (1943) how he observed Wood Thrushes (Hylocichla mustelina) go through the actions of rubbing ants on the breast, belly and flanks before or after the typical movements on wings and tail. Close watching showed, however, that the birds did not actually touch the feathers. Further, no species is known for certain to place live ants deliberately in the feathers with the bill, as has been maintained by some observers.

Birds “ant” extremely rapidly, then, and with marked concentration when performing at full intensity. They may continue the behaviour for several minutes, sometimes as long as half-an-hour. Many species show no obvious fear when approaching the ants and picking them up, but a few tropical birds are cautious. A typical anting-sequence proceeds likes this. The bird seizes a worker-ant in the tip of its bill, at almost the same instance contorting with swift movements into the anting-posture. One wing is lifted forward and sideways away from the body, carpal raised, the primaries spread and often brushing the ground. The tail is usually opened a little and jerked forward to the same side as the raised wing; sometimes so vigorously and so completely that the bird loses its balance, especially if it treads on it. Still in the very second that it picks up the ant and twists itself into position, the bird strokes the insect with a fast, flicking action down the underside of the extended wing, moving from near the base of the feather to the tip. In Ivor’s experience (1956), only the ant and perhaps the tip of the bill come into contact with the feathers, but Poulsen (1956b) found that parts of the head are sometimes also rubbed among the feathers. A series of strokes may be made under one wing, one primary feather being dealt with at a time, and then attention given to the other wing; or the bird may alternate more frequently from wing to wing. As may clearly be seen in Fig. 1, the angle of the outer primary feathers is often changed from the normal so as to present them edge-ways for easier treatment. The tail is also dealt with, the same actions being used in anointing the rectrices as with the flight feathers. Whether the tail happens to be stroked or not, it is usually contorted all the same, sometimes in rhythm with the rubbing movements on the wing; similarly, while the bird treats the tail, it still holds out the wing.

Ivor (1943) stated that the bird half-closes the eyes when anting and later (1956) showed that the nictitating membranes also flick across, as I also observed (Simmons, 1955). Ivor considers that this habit protects the eyes against formic-acid and against contact with the feathers.

There are variations in this typical anting procedure. Whereas the ant is usually crushed before being used, so that the acid-
glands are ruptured, intact insects are also sometimes employed. Most birds bite the ant quickly and then use it immediately, but a few nibble it carefully first. Some birds use only one insect for a single stroking movement; others perform several rubs at a time before getting a fresh one. Most use a single ant; a few collect several and use them all at once. Many remain among the ants while performing; others are more cautious and retire to a perch. Many eat at least some of the ants used; a few discard them after. While some of these differences are individual, most are probably specific. For instance, Pekin Robins nearly always use a single ant for a series of movements and Starlings (*Sturnus vulgaris*) always "ant" with a ball of crushed insects (Fig. 2), as

**FIG. 1—ACTIVE-ANTING BY AMERICAN ROBIN (*Turdus migratorius*)**
(Drawn by Robert Gillmor from a flash-photograph by Bruce R. Young)

Both this bird and the Starling (*Sturnus vulgaris*) shown in Fig. 2 are in the typical anting posture with one wing raised, tail spread and brought forward; the nictitating membranes are drawn across the eyes. Both birds are applying ants to the tail (the American Robin with one insect in its bill, the Starling with several); when ants are being applied to the wing, this is held more fully away from the body than shown here.)
often do the Magpie (*Pica pica*) and Blue Jay (*Cyanocitta cristatus*). Poulsen points out that there are not wide individual differences in anting-behaviour. Most of those that do occur are intensity variations. Thus, sometimes the full anting-posture is not assumed or,

![Active-anting by Starling](image)

*Fig. 2—Active-anting by Starling (Sturnus vulgaris)*

(Drawn by Robert Gillmor from a flash-photograph by Bruce R. Young)

*See caption to Fig 1.*

while the wing-movements are complete, the tail may not be brought forward. Often, too, birds which usually eat ants while anting may reject them during particular spells. In fact, it seems very probable that rejection of the ants is, at least in those species which also eat ants, a sign of really high-intensity anting (see pages 416-417).

Unlike all other Passerines but the Purple (Bronze) Grackle, some corvids rub ants on other regions of the body in addition to the conventional areas. The Magpie, for example, "ants" on the rump, base of the tail and in the area of the vent (Goodwin, 1953; Simmons, 1955). The Purple Grackle has a very characteristic manner of anting. It rubs ants among the feathers of the breast,
scapulars, rump and upper tail-coverts (Brackbill, 1948; Poulsen, 1956b), seeming to "dig" into the plumage with the insect in its bill, as when really preening, rather than to make the typical stroking anting-actions. It usually discards the ants afterwards, tossing them away as other troupials have been seen to do.

Some species bring forward both wings when anting. Poulsen (1956b) records this from the Blue Sugarbird (Dacnis cayena: Family Coerebidae). "This species picks up an ant in its bill, and very rapidly it rises in an almost vertical position with spread tail and moves both wings forward so that they touch each other while quivering, and the head is moved downwards among the tips of the wings". The sugarbird does not bring the tail forward while anting. The Azure-winged Magpie (Cyanopica cyanæa) also regularly advances both wings simultaneously (Goodwin, 1953) and the Blue Jay does so occasionally (Poulsen, 1956b), though otherwise both species "ant" normally.

The anting-behaviour of the Jay (see Fig. 3 and plate 62).

Our own Jay, and a few other foreign corvids, have anting-movements quite distinct from those of other Passerines (Goodwin, 1951, 1952, 1953):

"The main difference is that the common Jay does not pick up ants in its bill whilst anting (except sometimes to pluck them from its legs and cast them aside) although it makes the same movement of running its bill down the inner edges of its primaries and
secondaries as birds that do” (1952). “Both wings are thrust forward at once, the primaries brushing the ground, and (at high intensity) almost fully spread, so that they form a tent around and in front of the bird. This bringing forward of the wings is accompanied by a convulsive shuddering movement” (1953). “Needless to say, before the anting has gone very far the Jay’s whole plumage is a seething mass of ants which have swarmed up legs, wings and tail. How the bird can stand it is astonishing, and indeed its whole demeanour suggests a scarcely bearable irritation” (1951).

Only the Green Magpie (Cissa chinensis) and the Red-billed Blue Magpie (Urocissa erythrorhyncha) are known to “ant” in

**Fig. 4—Passive-anting by Carrion Crow (Corvus corone)**

**Fig. 5—Passive-anting by Carrion Crow (Corvus corone)**
(Both figs. drawn by Robert Gillmor from photographs by Hans Löhrl; mainly in outline in order to show posture clearly)

The bird lies down among the ants with wings and tail spread (often more fully than shown here) and allows the insects to swarm over it. The bird in Fig. 5 is possibly applying an ant to its rump, as this species is known to do.
the same way. All three species often bring the tail forward, though not invariably. Anting in the Jay has also been studied (with photographs) by Löhrl (1952, 1956).

*Passive-anting* (see Figs. 4-8).

While, strictly speaking, the behaviour of the Jay comes under this category, typical passive-anting differs appreciably. It has only been recorded from a minority of larger Passerines, mainly crows and thrushes of the genera *Corvus* and *Turdus* respectively, all of which also “ant” in the active manner, with the possible exception of the American Crow (*Corvus brachyrhynchos*).

The Carrion and Hooded Crows (*C. corone* and *cornix*) and the Rook (*C. frugilegus*) “wallow” in ants, flopping, grovelling and lying still among them with the wings outspread, tail raised or pressed down (Figs. 4 and 5), allowing the insects to swarm over (see, for example, Wackernagel, 1951; Goodwin, 1953, and Löhrl, 1956). Those thrushes that have been reported “ant-bathing” in a somewhat similar fashion include the American Robin (*T. migratorius*), Song Thrush (*T. philomelos*) and Redwing.

![Fig. 6—Passive-anting by American Robin (*Turdus migratorius*)](image-url)

This bird is showing the intention of anting passively, bringing forward both wings before settling down among the ants.
(T. musicus) (Poul sen, 1956b; and others). Apparently, Starlings may occasionally show this form of anting, judging from a single field-observation (Baggaley, 1946).

A certain amount of active-anting sometimes accompanies the passive (and also often precedes and follows it). Poulsen's thrushes applied ants to the wing and tail while ant-bathing but the full active-anting posture with wing raised does not seem to appear, so perhaps only lower intensity active-anting is connected with the passive. More observation is needed.

**Fig. 7—Passive-anting by American Robin (Turdus migratorius)**

In Fig. 7, the bird is bringing forward both wings (a characteristic passive-anting movement), but also has its tail advanced (typical of active-anting). In Fig. 8, it has settled down more fully among the ants. Passive-anting may often be accompanied by a reduced form of active-anting.

**Fig. 8—Passive-anting by American Robin (Turdus migratorius)**

(Both figs, drawn by Robert Gillmor from photographs by Holger Poulsen)
Further aspects.

After active-anting especially, the bird usually wipes the bill carefully. Ivor (1943) noticed no normal preening after anting, but Goodwin (1955b, 1956) stresses that preening and bathing in water often follow and this is my experience with the Pekin Robin. Brackbill (1948) also observed preening following anting in the Purple Grackle. Poulsen (1956 and in litt.) saw neither bathing nor preening, however. All this is very puzzling and more work is needed.

Several authors have commented on the almost trance-like state of anting birds and their peacefulness. This situation seems mainly due to the great intensity of the anting performance and no greater significance than this need be attached. In fact, there are quite a few records of aggressiveness during anting: Williams (1948) observed squabbles in wild Starlings, Brackbill (1948) song and threat from wild Purple Crackles, while Poulsen's thrushes drove away other birds that came near them. Derek Goodwin tells me that dominant Jays have precedence over subordinates at the ant heap, often driving them away.

DO WOODPECKERS ANT?

Now that full descriptions of all true anting-behaviour have been put before the reader, the question whether anting does really occur in the Piciformes may be further examined. No expert on this group has yet recorded the behaviour while Groskin (1943) and Poulsen (1956b) observed that flickers (Colaptes auratus and C. agricola) ate ants without attempting any form of anting. The only records of woodpeckers performing are based on field-observation of the Green Woodpecker (Allsop, 1949; Standford, 1949) and the Wryneck (Stone, 1954). I believe that the birds concerned were not anting and this is also implied by Goodwin (1956) and Poulsen (1956b). Both these species are regular eaters of ants and it is understandable that misinterpretation of some behaviour other than anting should have occurred. The two Green Woodpecker records agree that ants were applied to the breast and under the wings, while the birds were feeding on the insects. In addition, Standford's bird called loudly. It seems possible that both birds were, in fact, picking ants off their bodies and "shoulder-rubbing" (see p. 404) after being squirted with acid, the one bird crying out in pain. (A sequence of a Green Woodpecker "shoulder-rubbing" appears in Heinz Sielmann's fine film on woodpeckers.) In the case of the Wryneck, the bird was shuffling along the ground with half-open wings and tail, apparently rubbing something into its plumage with the bill. Mr. Stone (in litt.) informs me that the day in question was extremely hot. It seems possible that his bird was trying to sun-bathe but was inconvenienced by ants which it picked off its plumage.

ANTING BY PASSERINES ON THE BRITISH LIST

Out of over 170 species of Passerines on the British List, only
twenty have so far been recorded as anting and, of these, only ten species have been observed anting within the geographical boundaries of the British Isles. Such native British records have been indicated by an asterisk in the systematic list below. I have also indicated under each species whether observations have been made on its anting in wild or captive birds, where this is known.

There are no records from any part of the world for any species of the following families represented on the British List:—Oriolidae (orioles), Alaudidae (larks), Certhiidae (creepers), Sittidae (nuthatches), Paridae (tits), Laniidae (shrikes), Regulidae (kinglets), Sylviidae (warblers), Prunellidae (accentors), Troglodytidae (wrens), Hirundinidae (swallows). Neither has any European species of Muscicapidae (flycatchers) nor of Bombycillidae (waxwings) been recorded as anting, though two Asiatic flycatchers of the genus *Niltava* (closely related to *Muscicapa*) and the Cedar Waxwing (*Bombycilla cedrorum*) of N. America are known to perform. The records of anting are as follows:—

**Family CORVIDAE**

*Recorded from fourteen species of which six are on the British List.*

**RAVEN** (*Corvus corax*).—Only active-anting recorded, apparently (Jacobsen, 1917; cited by van Iijzendoorn, 1952).

*CARRION CROW* (*C. corone*).—Both passive and active-anting observed, in captivity and in the wild (Lorenz, 1936; Condry, 1947; Wells, 1950; Goodwin, 1953; Simmons, pers. obs.; and especially (with photographs) Wackernagel, 1951; and Löhrli, 1956).

*HOODED CROW* (*C. cornix*).—So far only passive-anting recorded from captive birds by Heine (1929) and Coombs (1947).

*Rook* (*C. frugilegus*).—Both main forms of anting noted in the wild and in captivity (Chappell, 1949; Goodwin, 1953; Simmons, pers. obs.).

*MAAGPIE* (*Pica pica*).—A most interesting species which apparently only "ants" actively, often collecting several ants in the bill at once. Tame Magpies have been known to use burning tobacco. Anting recorded both in the wild and in captivity by Heinroth (1911), Chisholm (1944), Reynolds (1946), Schierer (1952), Goodwin (1953) and Simmons (1955).

*JAY* (*Garrulus glandarius*).—The peculiar behaviour of this species has been observed in both wild and captive individuals. Full details and references are given on pp. 408-409. Goodwin mentions that sometimes a Jay will "ant" rather clumsily and ineffectively amongst the foliage of trees.

**Family STURNIDAE**

*Anting recorded from eleven species of which two are on the British List.*

**STARLING** (*Sturnus vulgaris*).—There are numerous accounts of active-anting by this bird, both in the wild and in captivity, including Tebbutt (1946), Gregory (1946) and Williams (1948). Passive-anting apparently occurs rarely (see Baggaley, 1946), but further observations are needed.

**ROSE-COLOURED STARLING** (*S. roseus*).—Active-anting seen from two captive individuals in the Copenhagen Zoo (Poulsen, 1956b).

**Family FRINGILLIDAE**

*Anting recorded from twenty species of which three are on the British List.*

**HAWFINCH** (*Coccothraustes coccothraustes*).—Active-anting reported by Poulsen (1956b) from two captive birds.

**CHAFFINCH** (*Fringilla coelebs*).—Active-anting recorded in the wild (Longhurst, 1949; Goodwin, 1955b) and in captivity (Poulsen, 1956b).

**BRAMBLING** (*F. montifringilla*).—Active-anting observed by Poulsen (1956b) from two captive individuals. Ivor's (1941) Brambling was not seen to "ant".
(N.B.—No members of the other finch genera represented on the British List (Chloris, Carduelis, Serinus, Pyrrhula, Carpodacus, Pinicola, Loxia) have been recorded anting, and Poulsen (1956b) mentions that his captive Green-finches (Chloris chloris), Linnets (Carduelis cannabina) and Canaries (Serinus canarius) did not perform although given the opportunity. No typical buntings (Emberiza, Calcarius, Plectrophenax) are known to “ant” either, though several other Emberizinae do so.)

Family PLOCEIDAE

Anting recorded from eleven species of which one is British.

*House Sparrow (Passer domesticus).*—There is only one record of anting in this widespread species—of active-anting from a wild bird (Common, 1956). The note by Davis (1945) obviously refers to dust-bathing, not anting. More records are urgently needed; Poulsen’s (1956b) Grey-headed Sparrow (P. griseus) did not “ant” although given the opportunity. The House Sparrow has one of the widest ranges of comfort-cum-cleaning behaviour of any species: it apparently “ants” occasionally, dust- and water-bathes, and also sun-bathes.

Family MOTACILLIDAE

Only one species known to perform anting and that is on the British List.

TREE Pipit (Anthus trivialis).—Active-anting observed in a captive bird by Poulsen (1956b).

Family TURDIDAE

Anting recorded from eleven species of which six are on the British List.

*Mistle Thrush (Turdus viscivorus).*—Only active-anting recorded so far; from wild birds (Abma, 1951).

*Song Thrush (T. philomelos).*—Both forms of anting observed in the wild (Stresemann et al., 1935; Chisholm, 1944; Gough, 1947; Wells, 1951; Fitter and Richardson, 1951); and passive in captivity (Poulsen, 1956b).

*Redwing (T. musicus).*—Both active and passive-anting recorded by Troschütz (1931) and Poulsen (1956b) in captivity.

*Ring Ouzel (T. torquatus).*—Active-anting mentioned in Wackernagel (1951).

*Blackbird (T. merula).*—Only active-anting so far reported from this apparently infrequent “anter” (Williams, 1947; Logan Home, 1954; Tenison, 1954; D. W. Snow, pers. comm.; Simmons, pers. obs.). Ivor’s (1943) Blackbird was not seen to “ant”, and all the other records are of wild birds.

*American Robin (T. migratorius).*—“Ants” both actively and passively (Nichols, 1943; Ivor, 1956; Poulsen, 1956b). Ivor’s birds were never observed performing passive-anting completely, though one spread its wings as if to do so on one occasion (see, Fig. 6).

(N.B.—The distribution of anting in the thrush family is rather peculiar. So far the behaviour has been noted mainly in the large birds of the genera Turdus and Hylocichla; and apart from that, only in the Magpie-Robin (Copsychus saularis) and the Shama (Kittacincla malabarica), two medium-sized species. No wheatears and chats (Oenanthe, Saxicola, etc.), redstarts (Phoenicurus), nightingales and bluethroats (Luscinia and Cyanosylvia), or the Robin (Erithacus rubecula) and allied species have been seen performing. Poulsen (1956b) gave two Redstarts (Ph. phoenicurus), a Nightingale (L. luscinia), two Robins, one Pied Bush Chat (Saxicola caprata) and an Indian Robin (Saxicoloides fulicata) the opportunity, with negative results, though all ate the ants.)

Family CINCLIDAE

One record of anting only, from a species on the British List.

Dipper (Cinclus cinclus).—Active-anting recorded by Heinroth (1911) and Braun (1924) from captive birds.

ANTING IN OTHER EUROPEAN PASSERINES

Only one more native European bird is known to “ant”, the
Azure-winged Magpie (see p. 408), but the following American vagrants do: the Catbird (*Dumetella carolinensis*, Family Mimidae); the Hermit Thrush (*Hylocichla guttata*), the Slate-coloured Junco (*Junco hyemalis*, Family Fringillidae); and the White-throated Sparrow (*Zonotrichia albicollis*, Family Fringillidae).

**ANTING AS INSTINCTIVE BEHAVIOUR**

It is evident from their stereotyped nature that anting-movements are innate, not acquired by learning. This is supported by observations on a few birds known to be anting for the first time and to have seen no others performing (see Nice, 1943; Goodwin, 1952; Poulsen, 1956b). Inexperienced birds "know" how to "ant", but seem to have to learn for certain that ants themselves are the correct objects to use, the taste of the insects probably being the major factor. Some observations (e.g. Condry, 1947) indicate, however, that there is at least a slight predisposition to recognize ants as the correct objects, but that this has to be reinforced by experience. On this basis, it is not hard to understand that quite a variety of other items, caustic in nature, are used on occasions by anting birds besides the conventional acid-carrying work-ant. Osmaston's (1909) hand-reared babblers used pungent-smelling bugs (*Rynchota* sp.; Hemiptera), and the literature is full of instances of strange substances being employed, "usually of an apparently irritant nature such as tobacco ash, lighted cigarettes, mothballs, small limes, and various insects" (Goodwin, 1955b). To this list, Nice (1955) adds hot chocolate and soap suds, but perhaps the most spectacular case* concerned a tame Magpie which would collect a bill-full of ants, fly indoors, dip them into the bowl of a lighted pipe and rub the mixture under the wing (Chisholm, 1944). As early as 1911, Heinroth had recorded this species anting with cigar butts.

On occasions, experienced birds may show anticipatory anting-movements merely on seeing the insects. Also, they may use acid-less male "flying" ants and ant-species which do not produce any acid. Poulsen (1956a and b) sprayed captive birds with formic-acid (and also citric-acid and formalin) in order to induce them to "ant". If these liquids reached the birds' breasts or backs they merely shook their plumage and flew away; but when they were squirted on the head, they then performed intense anting-movements. A Jay, already anting when Poulsen sprayed it, "made incipient anting movements and sometimes complete anting" when he stood by its cage with the sprayer unused in his hand some hours later.

Partially on the evidence just mentioned, Poulsen is of the opinion that active-anting is performed "unintentionally", merely as a reaction to acid or other irritants on the head. However, most authorities on anting believe otherwise. Poulsen states in further support of his theory that there is no indication of the waxing and waning of an internal anting "drive". Birds studied

*Since this was written, Burton (1957) has described (with photographs) how a Rook performed both kinds of anting in fire.
by him ate ants and also anted every day (sometimes several times daily) for more than a month. On the other hand, he did find evidence that passive-anting was internally motivated, the birds concerned anting only when they were in anting "mood". However, the work of Goodwin clearly indicates fluctuations in the tendency to perform both kinds of anting. Although ant-eating is common (at least in aviary birds), anting itself is more rarely shown. "Whereas captive insectivorous birds are nearly always eager for live insects . . . it may be weeks before they are eager to ant again after having indulged" (Goodwin, 1955b). Some species, or perhaps more accurately some individuals, "ant" extremely rarely. Thus, Ivor's (1956) Evening Grosbeaks (Hesperiphona vespertina) and Cedar Waxwings were only seen to "ant" once in nearly eighteen years of observation. Goodwin's (1955b) Lanceolated Jays (Garrulus lanceolatus) performed when first given ants in 1951 but not again subsequently, and his tame Magpie never anted during the three years he had it—yet individuals of both species in the London Zoo anted keenly on each occasion he gave them Wood Ants. Evidence of this sort does not support Poulsen's theory which implies that active-anting is really no more than a reflex, that is an automatic reaction to external stimuli, not influenced by central nervous processes. A bird anting intensely and protractedly, seeking the ants and selecting workers, using and then often rejecting them afterwards, certainly does not convey that its behaviour is only unintentional. Poulsen's theory also implies that the two forms of anting are unrelated, but this seems very doubtful as the two may often be performed together and intermediate behaviour occurs.

Anting-behaviour of both types does seem, rather, to be true instinctive-behaviour in the modern sense. The very fact that we can observe intensity variations, although the external factors are not altered appreciably, strongly suggests that all anting-behaviour is really instinctive, that is governed by both external and central-nervous factors. Poulsen's work clearly shows, though, that anting is one of those behaviour-patterns greatly influenced by external stimuli (bathing in water, preening and head-scratching are others)—but that is not the whole story, of course. Anting possesses all the variable characters of instinctive behaviour. For example, if the internal tendency to "ant" is strong, then the bird may do so with inadequate objects ("ant-substitutes", male ants, etc.) or start anting merely on seeing the workers ("anticipatory anting"—wrongly termed "vacuum-anting" by Simmons, 1955). Conversely, if strong external stimuli associated with anting are present, this may induce a bird to "ant" even though it were not previously in the mood. Poulsen's spraying experiments may be interpreted along these lines. Anting-behaviour does seem to be a more or less independent pattern with its own specific motivation, perhaps belonging to the same group of behaviour-patterns as preening and bathing (see below).
it is often associated with feeding does not necessarily mean that this connection is a fundamental one. Anting and feeding share a common causal factor in this case—ants. Frequently the two tendencies do not inhibit each other and a bird can "ant" and eat the insects during one session. Often the tendency to feed is stronger than that to "ant" because, in addition to the worker-ants, the more edible larvae are present, especially under aviary conditions (see also pp. 403-404). However, all the evidence suggests that, when the urge to "ant" is very much stronger than that to feed, then anting will predominate, the birds often discarding the ants without eating them.

THE ORIGINS OF ANTING-MOVEMENTS

Active-anting has all the characteristics of "derived activity", that is of a behaviour-pattern adapted and modified from existing ones by natural selection in order to serve a new purpose. Most derived behaviour has a signal (display) function (see Tinbergen, 1952), but active-anting is one of the relatively few conspicuous exceptions, the dust-bathing of the House Sparrow being another (Simmons, 1954). Like Poulsen (1956b), I cannot agree with Chisholm (1944) that this form of anting may have originated from birds' dust-bathing in the loose earth on the surface of ant-colonies, for a comparison of the respective movements does not confirm this. The dusting behaviour of the sparrow contains elements similar to bathing in water and to nest-shaping, while anting is most like preening.

The more extensive anting of some crows and, especially, of the Purple Grackle supports the possibility of a link between anting and preening. The grackle actually "digs" the ants into its contour-feathers with motions very similar to preening. The anting-like behaviour of certain non-Passerine Australasian lorikeets (Trichoglossus spp.) is also suggestive. These parrots chew Eucalyptus shoots and get the volatile oil on their bills. They then obtain further oil from the preen-gland and preen the tail, breast, belly, under-wing, back, mantle, wing-coverts and flight-feathers—always in that order (Harwood, 1955).

The typical, more restricted movements of active-anting are in several ways similar to normal preening (especially to the rapid preening before and after water-bathing) and very probably derive from this (Simmons, 1955; Poulsen, 1956b). There are elements common to both anting and preening, including the raised posture of the wing, the spreading and sideways movement of the tail and the method of dealing with the feathers from base to tip. The differences seem in part due to the entirely separate situation in which each is performed. When anting, the bird does not seize hold of its feathers in the bill, and a new factor—the ant—is present. Otherwise anting differs from preening mainly in that its movements are more extreme and are co-ordinated differently, both common characters of derived behaviour. In preening, the
wing and tail are never brought forward together or so completely as in anting. Poulsen (1956b) points out that an anting bird, supposedly never like a preening one, sometimes rubs its head amongst the wing-feathers. However, a similar movement occurs when a bird applies preen-oil, a not insignificant parallel. Precisely in what manner active-anting has arisen from preening is not yet clear, but there is no reason to suppose that it was originally a displacement-activity.

It seems strange that most birds "ant" only on the underside of the outer primaries and rectrices. As pointed out by Brackbill (1948) and others, these feathers are the stiffest parts of the entire plumage. Their rigidity is increased further by the anting-posture itself, in which the wing often touches the ground while the tail lies along it. These are, therefore, the ideal areas on which to rub ants in order to extract acid efficiently and rapidly. Being most remote from the tracts of skin, they are also the safest areas and their use, then, may have evolved because rubbing the insects on other parts was mainly ineffective and/or unpleasant, or even dangerous. Possibly today's active-anting movements are mere relicts of a once more widespread anointing which proved harmful in some way and was reduced by natural selection. Now, only the larger species can practice a more elaborate anting. Some foreign species show a precaution bordering on fear when anting even with relatively harmless ants; this suggests that they might use, or at least on occasions be likely to encounter, ants that are potentially dangerous. Observations on tropical driver-ants (for example Elliott, 1950) are of great interest in this connection. Birds follow the foraging swarms and prey on the insects disturbed by the lethal soldier-ants, showing much fear of the latter. Should an attending bird get among the ants, then it may be swiftly killed. The largest species of British ant is the Wood Ant which may conceivably be capable of hurting smaller birds if applied unreservedly. Perhaps, also, larger and more deadly ants were present in the past when anting first evolved. It seems possible, too, that anting first appeared in tropical or semi-tropical representatives of our Passerines for, today, anting is more widespread in bird species of the warmer regions.

Unlike the active-, the distinct passive-anting movements are not apparently derived from other behaviour, though Rothschild and Clay (1952) are of the opinion that these might have evolved from sun-bathing. There are, in fact, certain resemblances between the "spread-eagle" versions of the two, but this seems to be due to convergence. Both postures function to expose the maximum area of the bird to the desired object—ants and sun-rays respectively. Although less elaborate than the active, passive-anting seems in some ways more efficient in that it does expose a greater area of feathering to the formic-acid (and other exudations). If the theory that anting is (or was) potentially dangerous be correct, then the facts that only larger Passerines perform the
passive kind, and also alone use bill-fulls of insects, make considerable sense.

THE FUNCTION OF ANTING

The biological significance of anting is a most controversial topic; it is still largely uncertain why birds perform “this most improbable” behaviour, as van Tyne (1943) calls it. The current theories have been reviewed in detail by Wackernagel (1951) and by van IJzendoorn (1952) but, as Poulsen (1956b) points out, none are really quite convincing. Several, indeed, are quite unsound and will not be discussed (for instance, it has even been suggested that birds place ants in their plumage as food-reserves for long journeys).

The most popular theory is that anting is of some use in “the destruction or discouragement of ecto-parasites” (Goodwin, 1955b), though there is still no positive evidence for or against. Ivor (1956) has pointed out that if this insecticide theory is correct, then it is strange that the anting bird does not “rub deep under its wings and other parts of its body where parasites are most likely to gather” and this criticism has been repeated by Poulsen (1956b). However, the grackle and some crows do practice a more extensive anting, while passive-anting gives the insects access to all parts of the plumage. The restricted natures of most active-anting may be accounted for along the lines put forward in the last section and, in any case, as Goodwin has stressed, the formic acid may assist in combating the parasites during “the bathing and vigorous preening which usually follow anting”. Ali (1936) elaborated the ecto-parasite theory and suggested that the consumption of the crushed worker-ants and their acid might be of use against endo-parasites. However, such a function could be achieved merely by the eating of ants.

Chisholm (1944) and Wackernagel (1951) think that birds “ant” in order provide the skin with a tonic stimulant, while van IJzendoorn (1952) subscribes to the theory that they derive pleasure and exhilaration from the experience, similar to that which man gets from alcohol. Both these functions are not improbable, yet surely must be subsidiary? It is difficult to believe that natural selection could have produced such an unlikely and potentially dangerous pattern, which increases the birds’ conspicuousness to predators and exposes them in certain cases to harmful insects, unless there was some more important function.

If Poulsen’s theory of the reflex nature of anting should prove correct, the puzzle of the biological significance of anting is greatly simplified. Active-anting, then, simply functions in allowing the bird to avoid the discomfort of irritation on the head. When Poulsen first advanced this idea at the XIth International Ornithological Congress at Basle in 1954 it was enthusiastically received by Huxley (1954) and others. It has, however, been criticized by Goodwin (1955a and b), Simmons (1955) and by
Ivor (1956), while further arguments against are given and implied here. Long before Poulsen’s work was done, Adlersparre (1936) and Steiniger (1937) had suggested that birds “ant” merely to clean the food of acid before eating. This was also well received, by Stresemann (editorial comment to Adlersparre’s note), but subsequently criticized by Chisholm (1944). Such a theory again supposes that when a bird “ants” it is primarily motivated by a feeding tendency and this does not accord with the facts. Poulsen (1956b) has also put forward another suggestion—“It is of survival value at least for some insectivorous birds that they have a means, viz. anting, by which they are able to overcome the defence from their prey”. However, birds usually incapacitate harmful insects in quite different ways: by banging them on a hard object, such as a branch, and/or by biting them quickly and then dropping them immediately, continuing this until the insect is dead. All the other facts about active-anting also speak against this view.

My own opinion, briefly mentioned elsewhere (Simmons, 1955), is that anting is of value in achieving a more efficient preening, including the removal of feather-parasites if present. This is supported by the probable connection between active-anting and true preening and by the fact that both forms of anting are often followed by bathing and preening, during which the acid could be distributed over many feathers. It seems very possible that formic acid may act in some ways similar to the bird’s own preen-oil. This has been discussed by Brackbill (1948) who quotes an important and little known note by Kelso (1946). The latter suggested that oil was spread on the feathers for the purpose of irradiation, vitamin development and later ingestion through preening; Formic acid (and other exudations) might function, then, in a similar or even superior way when “affected by exposition to natural or artificial ultra-violet radiation”.* One of the primary functions of anting may be the disposal of stale oil from the plumage and the general improvement of the tone of the feathers.

**FUTURE WORK ON PROBLEMS OF ANTING**

Much yet needs to be discovered about anting, as often indicated in the body of this paper. Actual precise description is mainly the task of the aviary observer who is at a distinct advantage in this subject. He can make careful studies on individual species to show specific differences which have tended to be obscured in the general summing-up. He can also experiment. We need as many records as possible for additional species from all parts of the world. The value of anting from the point of view of the classification of the Passerines (and especially of the Fringillidae) needs to be examined and this can only be done if records—both positive and negative—are available for many

*There is, so far as I know, no evidence of a link between the performance of anting and sun-bathing, as implied by Brackbill.
groups. A brief report on taxonomic aspects of anting has been prepared for publication elsewhere. The rôle of the field observer is an important one, too. One of the most valuable papers on anting, that of Brackbill (1948), was based on observations of wild birds. More records are needed of anting in the wild, especially on the circumstances in which birds “ant” naturally (a subject about which we know very little), the ant species used (an aspect not covered in this paper) and their activity, and so on. A particularly useful study would involve the watching of certain colonies of ants and recording all the reactions of birds to them, including avoidance and feeding, so that, among other aspects, some idea of the frequency of anting could be obtained.

It is not easy to observe wild birds anting under entirely natural conditions. I have seen the performance only twice in the field, from a Jay and a Rook*, and my views were so fleeting that it would have been impossible for me to describe the behaviour from those observations alone. However, it is not necessary to wait for an opportunity to come; anyone keen to see an anting session can deposit a large heap of active Wood Ants (plus nest debris) in a suitable spot and is guaranteed an enjoyable and fascinating time, especially if any Starlings are in the neighbourhood. When publishing records, all important details should be given, such as whether ants were in fact seen in the bill, so that the validity of the observations can be judged by future workers. Care must be taken that it is indeed anting that is being observed. Some of the activities that could conceivably be mistaken for true anting include: (1) eating of ants, (2) dust-bathing, (3) preening, stretching and the scratching of the head, (4) sun-bathing, (5) shoulder-rubbing (see page 404), (6) picking ants off the body. If the present review has equipped observers to recognise and make worth-while studies on anting-behaviour, then one of its chief aims will have been achieved.

SUMMARY

This paper is a critical review, with bibliography, of the anting-behaviour of birds. True anting takes two main forms: active (the bird applies crushed ants to the underside of the wing and tail with its bill) and passive (the bird allows live ants to crawl on to its plumage). These, and intermediate behaviour and variations, are described in detail and seem confined to Passerine birds, well over one hundred species of which have now been recorded as anting. Of these, twenty are on the British List, of which only ten have been seen performing within the geographical boundaries of the British Isles. Woodpeckers and game-birds almost certainly do not “ant”, as has been claimed.

Both forms of anting have many characters of true instinctive-behaviour and possibly function in effecting a more efficient preen-

*And, since the above was written, from a Blackbird.
ing. In fact, active-anting probably derives from preening-movements.

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Anting-behaviour is confined to the Passerines, of which the majority, including the present species, "ant" actively by rubbing ants along the underside of the wing and tail while assuming the special posture shown here (see pages 401-424). Unlike some *Turdus* thrushes, to which it is closely allied, the Wood Thrush does not, so far as we know, "ant" passively by lying down and allowing the insects to swarm over the plumage.
BLUE JAY (Cyanocitta cristata) ACTIVE-ANTING
This species (here treating its left wing) frequently “ants” in the active manner. Note how the angle of the outer primaries has been changed to make the feathers more accessible.
The Blue Jay (Cyanocitta cristata) active-anting.
The Blue Jay often uses a single ant, but sometimes collects several. As is usual, the nictitating membrane is drawn over the eye to protect it. The anting of this species is not always quite typical for both wings are occasionally brought forward.
The American Robin is one of the few species that "ant" by both the active and passive methods (see Figs. 6-8, pages 410-411). Here (lower) the bird is rubbing an ant on the underside of the tail which has been brought forward very sharply indeed. These and the other photographs by Messrs. Corby and Young were taken, with the aid of electronic flash, at H. R. Ivor's song-bird observatory in Canada.
This species is a very ready "anter". Unlike most species, it collects up a whole bill-full of insects to use (see Fig. 2, page 407). The upper plate shows an unusually full version of the posture employed to rub ants under the wing. These and the other photographs by Mr. Young are taken from beautiful colour-transparencies which have lost much of their clarity by being printed in black-and-white.
The anting-behaviour of the Jay combines elements of both active and passive forms. While this species does not pick up ants, it does go through the motions of rubbing them on the underside of the wings, both of which are spread forward to allow the insects to swarm up over the plumage. Although not shown above, the tail is often brought forward (see Fig. 3, page 408).