A RÉSUMÉ OF ANTING, WITH PARTICULAR REFERENCE TO A CAPTIVE ORCHARD ORIOLE

BY LOVIE M. WHITAKER

Since Audubon (1831:7) wrote of Wild Turkeys (*Meleagris gallopavo*) rolling in "deserted" ants' nests (Allen, 1946), and Gosse (1847:225) reported Tinkling Grackles (*Quiscalus niger*) in nature anointing themselves with lime fruits (Chisholm, 1944), an extensive literature on the anting activities of birds has slowly evolved. The complete bibliography of anting probably would approximate 250 items, yet the purpose of the behavior remains unexplained.

Anting may be defined as the application of foreign substances to the plumage and possibly to the skin. These substances may be applied with the bill, or the bird may "bathe" or posture among thronging ants which invest its plumage.

Among numerous explanations for the use of ants are these: (1) the bird wipes off ant acid, preparatory to eating the ant; (2) ants prey upon, and their acids repel, ectoparasites; (3) ant acids have tonic or medicinal effects on the skin of birds; (4) odor of ants attracts birds, much as dogs are drawn to ordure or cats to catnip; (5) ants intoxicate the bird or give it unique pleasurable effects; (6) ant substances on the plumage, irradiated by sunlight, produce vitamin D, which the bird ingests during preening; (7) the bird enjoys the movement of insects in its plumage; (8) ant substances prevent over-drying of feather oils or give a proper surface film condition to the feathers. For discussions of these possibilities, see Chisholm (1944, 1948: 163-175), Adlersparre (1936), IJzendoorn (1952a), Eichler (1936a), Kleinschmidt (in Stresemann, 1935b), Lane (1951:163-177), Kelso (1946, 1949, 1950a, 1950b, 1955:37-39), Brackbill (1948), Géroudet (1948), Groskin (1950), and McAtee (1938).

At least 24 kinds of ants and more than 40 substitute materials have been used by anting birds. These materials include fruits, foliages, raw onion, burning matches or tobacco, gum of grass-tree (*Xanthorrhoea preissii*), millipedes (Diplopoda), various beetles ("weevils"; tenebrionid beetles of the genus *Blaps*), grasshoppers (*Anacridium aegyptium*), earwigs (*Forficula*), bugs (*Rhynchota* sp., *Rhaphigaster nebulosa*), wasps, hair tonic, prepared mustard, vinegar, hot chocolate, and moth balls (Ivor, 1941; Laskey, 1948; Parks, 1945; Robinson, 1945; Thomas, 1946; Groff and Brackbill, 1946; Baskett, 1899:243; Burton, 1955a, 1955b, 1955c; Chisholm, 1944, 1948:163– 175; Sedgwick, 1947; Poulsen, 1955, 1956; Sedgwick, 1946; Adlersparre, 1936; Osmaston, 1909, 1936; Callegari, 1955; Govan, 1954; Freitag, 1935; Butler, 1910; McAtee, 1938; Fluck, 1948; Scheidler, in Stresemann, 1936; Nice, 1952, 1955a; Hill, 1946; and others).



Female Orchard Oriole (*Icterus spurius*) engaged in anting. Photographed by Arthur A. Allen, at Norman, Oklahoma, on January 14, 1955.

A compilation of records shows that at least 148 species of birds, 65 of them New World forms, are reported to introduce ants, or their so-called substitutes, into or on the plumage. Included is the Wild Turkey, so far known only for dusting in defunct ant nests (Allen, *op. cit.*, citing Audubon; McAtee, 1947, citing Sharp). Not included are several other species, to be mentioned later, that are known to use smoke but not ants or other substitutes.

Among the 148 anting birds listed in Table 3, the first 16 are non-passerines. The Horned Owl and all but one species of the Phasianidae listed dusted in activated ant beds or were seen to have live ants in their plumage. The Scaled Quail (*Callipepla*), the parrots, the Wryneck (*Jynx torquilla*) and the Green Woodpecker (*Picus viridis*) applied ants or a substitute with the bill.

The belief that anting is restricted to passerines has been rather general, and reports of anting among other groups of birds sometimes have been questioned or discounted altogether. Inquiries and search of the literature, however, reveal a notable amount of little known or entirely new data on a number of species, including non-passerines. Evidence for picids now is substantial, as will be seen; and we can reasonably expect further records for other species whose status as performers of anting still may seem suspect to some investigators.

During my visit to Chiapas, Mexico, in July, 1956, Miguel Alvarez del Toro, Instituto Zoológico del Estado, Tuxtla Gutierrez, furnished me with data on five Mexican species he had seen anting in nature. One of these, the Goldenfronted Woodpecker (*Centurus aurifrons*), used a small species of papermaking wasp common in that region. Specimens of the wasp, received from Dr. Alvarez in March, 1957, have been identified by K. V. Krombein, Smithsonian Institution, as *Polybia occidentalis* (Oliv.), a very gentle social species in which only the females have a sting. Wasp venom in general is supposed to contain formic acid.

Still another record for a picid comes from Fred M. Packard, Washington, D. C., who advises me that he has seen anting in the Flicker (*Colaptes auratus*) in New Jersey (letter, July 18, 1955).

Those who hold that non-passerine birds never are anting when they dig into, and dust themselves with, ant-nest earth containing large numbers of agitated, aggressive ants, may not accept Mowat's (1957) interpretation as "ant bathing" for his tame Horned Owl's habit of "tearing an anthill apart and then fluffing the mixture of dust and angry ants through his feathers." Mowat (letter, April 29, 1957) states that the owl regularly engaged in the activity on hot summer days, using the nests of unidentified, small, red lawn ants. "He appeared to brood over these nests, after stirring them up with his talons, and would sit for as much as half an hour without apparent movement. . . . He showed no signs of ecstasy, or stimulation. In fact, he usually appeared to be asleep." Through the courtesy of Edwin Way Teale (1953; letter, February 6, 1955), I have the statement of Stanley Dashuta of Newark, New Jersey, who many times has seen Ring-necked Pheasants scratch down ant hills. This observer noticed hundreds of ants swarming over the birds and saw many injured ants on the ground afterward.

Robert W. Darrow (Bump *et al.*, 1947:272; letter, November 18, 1955) found that Ruffed Grouse used both deserted and active ant nests, but in most cases dusted in unoccupied nests or those with small populations. Nevertheless, it is by no means certain that this bird, or other birds, dusts in ant beds *only* because these offer a ready supply of loose, light soil. There is some evidence that a bird may be sensitive to special properties in the dusting soil and that anting and dusting may be more closely allied than was suggested by Chisholm (1948:163–175).

Howard Campbell (1954) has shown how Scaled Quail (*Callipepla squamata*), and possibly also Gambel's Quail (*Lophortyx gambelii*), in four New Mexico counties, where dusting opportunities would seem to be optimal, were strongly attracted by places where old motor oil had been spilled. A substantial number of 46 such experimental oiled dust baths were found to have had heavy and continuous use. In a suitable dusting area, the birds chose the oily spots, and they worked even in an area of extremely coarse gravel which had been oiled. Mr. Campbell wrote me that the birds seemed to use the centers of these oiled areas rather than the edges.

At my request, he made temperature readings on treated and untreated dusting areas, using a standard Taylor fisheries thermometer with the halfinch bulb barely buried in the earth. A larger series of readings is needed, but his preliminary investigation shows that temperatures of oiled soils can be as much as 4° F. higher than those taken in adjacent areas.

Gibson (1954) described a White-winged Chough (*Corcorax melanorham-phus*) in Australia that did not dust normally, but instead puts beakfuls of dust into its body plumage and under the wings. The action so strongly suggested anting that Gibson, upon determining no insects were present, had the soil tested for formic acid, with negative result.

It has been argued, largely on the basis of Walter's (1943) work, that birds probably have little or no olfactory sense and that galliform birds, especially, would tend to be insensitive to ant odors. But Hamrum (1953) stated the literature on olfaction and gustation in birds is contradictory and confusing. His own experiments show that both odor and taste probably influence food choice in the Bob-white (*Colinus virginianus*). Thorpe (1956:306) cautioned against dogmatism regarding sense of smell, pointing out that birds "show a considerable range of development of the olfactory lobes" and that only a few forms have been studied critically.

Until more is known about the purpose and effect in birds that apply ants

with the bill, the assumption that anting is not to be found in the galliform or certain other groups of non-passerines (Goodwin, 1955b; Poulsen, 1956; IJzendoorn, 1952a) seems unwarranted. At this stage of investigation, it seems premature, even a little illogical, to say that a pheasant or a grouse, exposing its body to a host of disturbed ants on an ant nest, is not anting but only dust-bathing; while, at the same time, accepting as bonafide anting the behavior of certain corvids, to be mentioned later, that neither apply ants with the bill nor make dust-bathing motions but which stand or sit among ants with special attitudes of wings and tail while allowing ants to invest their plumage.

Closer study of Common Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*) should help resolve the question of anting in game birds. Starlings are known to work themselves deeply into the ant nest by use of the feet, bill and wings, and to apply ants deliberately under their wings (Floericke, 1911, and in Stresemann, 1935b; Baggaley, 1946). Davis (1945) noted a House Sparrow on an ant hill, dusting itself among the ants; and, in a letter to me, he emphasized that the bird also was using its bill to apply ants under the plumage in typical anting manner.

Cases combining dusting and applying ants with the bill, such as those cited above, are interesting also as possible transitions between "passive" anting (standing, sitting, sprawling among ants, but usually not applying with bill; see Fig. 5) and "active" anting (anointing only by use of bill). This distinction is made by Rothschild and Clay (1952:126–128).

It is unfortunate that the word *anting* is so deeply imbedded in the literature, since it does not have universal definition and is not always descriptive of the behavior. Thus we find McAtee (1938, and in Chamberlain, 1954) excluding the use of substitutes in defining anting; Goodwin (1955b) and Poulsen (1956) dismissing records of game birds using activated ant nests a behavior which McAtee accepts; and Ivor (1951, 1956) excluding such passive anting as that seen in Common Crow (*Corvus brachyrhynchos*). Despite these exclusions, it now appears that the term ought to include all anointings, whether active or passive, with ants or substitutes. Certainly this was the connotation given the term by Stresemann (1935b) in coining it.

Although anting is a major ornithological problem that no one has adequately explained, it has received relatively little experimental study. A new theory, offered by Holger Poulsen (1955), who experimented with 34 anting species in the Copenhagen Zoo, states that anting is caused by the ants' spraying of acid on the bird's head. The bird then rubs its head under wing or tail in an effort to remove the irritating acid. Poulsen, observing only active anting, and apparently questioning the many descriptions of passive anting, concluded that feeding was the basic incentive, and the anting actions incidental corollaries to it, as the bird tried to cleanse its head of ant acid or tripped about to avoid being sprayed. He considered tripping and falling, as well as reports of birds lying down among ants, all to be results of the bird's vigorous cleansing and evasive movements. Some investigators, however, found that this theory did not explain anting as they observed it (Nice, 1955b; Goodwin, 1955a, 1955b; Simmons, 1955; Ivor, 1956).

Since then, Poulsen (1956) continued experiments (involving 85 species in all, of which 56 species anted) and discovered that certain species would indeed deliberately expose their plumage to ant spray. But he still is of the opinion that, with few exceptions, anting is unintentional behavior connected with feeding, and that only such exceptional species (more or less passively anting birds, as defined here) seek ants in order to be sprayed, rather than to eat ants. While he does not use the terms, Poulsen makes it clear that he believes active anting to be a response to external stimulus and that passive anting evidently is motivated internally, depending upon the bird's being "in anting mood." He has no definite solution to the problem, and offers these explanations tentatively. In a letter (February 7, 1956) he stated that he regarded anting as a complicated behavior, with more than one biological significance.

In view of the many poorly understood, even puzzling, aspects of anting, it seemed that an intensive examination of the behavior in the individual bird, with various species of ants, might be at once interesting and worthwhile.

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ANTING IN A CAPTIVE ORCHARD ORIOLE

On September 18, 1952, I discovered my hand-raised, three-month-old, female Orchard Oriole (*Icterus spurius*) anting in a file of ants which had invaded a screened porch. Systematic observations on the bird began on March 23, 1953. In the following 31 months I made 80 experiments on as many days, using various ant species found in my yard. Excepting two experiments in which the ant *Tapinoma sessile* was used in September and October, 1955, at East Lansing, Michigan, all observations were made in Norman, Oklahoma, with indigenous ants.

Four other hand-raised individuals—Black-billed Magpie (*Pica pica hud-sonia*), Loggerhead Shrike (*Lanius ludovicianus*), House Sparrow, Painted Bunting (*Passerina ciris*)—did not ant, and only the Magpie and Painted Bunting would eat ants. These birds were tested at intervals during periods of two months or longer, the Magpie for over a year, while the Painted Bunting was the constant companion of the Orchard Oriole during the latter's anting experiences. Kuroda (1947) noted anting-like behavior in a captive Bullheaded Shrike (*Lanius bucephalus*); but there seems to be no report of anting in Painted Buntings, and I find but three for the House Sparrow (Table 3). It is strange that there should be no New World record for this race of Magpie, since the species is a well-known "anter" elsewhere (Table 3). In this connection, it is interesting to recall that Brooks (1931) suggested specific rank for *Pica p. hudsonia*.

For present purposes I shall apply the term *acceptable* to those ant species the Orchard Oriole used for anointing (Table 1), and *unacceptable* to those it rejected (Table 2), whether or not the species was eaten.

Lovie M. Whitaker

I found workers of three ant species, Dorymyrmex pyramicus, Iridomyrmex pruinosus analis and Tapinoma sessile were acceptable and also were eaten. Workers in these species are monomorphic. All are small (2 to 3 mm. in body length), non-stinging ants which feed on honey-dew and insects. Instead of spraying acid secretions when disturbed, these species exude from the anal glands fluid droplets having the scent of rancid butter. This odor, presumably due to butyric acid, is especially strong when the ants are crushed. Evidently these species, all belonging to the subfamily Dolichoderinae, do not produce formic acid. O'Rourke (1950) stated that "so far as is known, the Formicinae [i. e., Lasius, Formica, Camponotus, etc.; see Table 1] alone among ants secrete formic acid." For pertinent details on the ant species mentioned above and in the next paragraph, see also Wheeler (1910:29, 42–43, 45, 361), Creighton (1950:110–111, 162, 171, 210, 340, 346–348, 350–352), Cole (1940), Smith (1924, 1928), Dennis (1938).

The very small ants, *Pheidole bicarinata buccalis* and *P. b. longula*, and the small *Crematogaster (Acrocoelia) laeviuscula*, as well as the large *Pogonomyrmex barbatus*, were all unacceptable to the oriole, although both of the *Pheidole* sometimes were eaten. All the rejected ant species belong to the subfamily Myrmicinae. Workers of these species possess a sting. The sting in *Pogonomyrmex barbatus* is extremely painful to man; but that of *Pheidole* is too weak to penetrate human skin, as, in my experience, was true also of the *Crematogaster*. This particular *Crematogaster* feeds on honey-dew, dead insects and animal tissue; but ants of the genera *Pheidole* and *Pogonomyrmex* are largely spermophagous, though some *Pheidole* take insects and honey-dew, and *Pogonomyrmex* will eat insect food. None of the rejected species sprays or exudes repugnatorial liquids.

Neither the Orchard Oriole nor any of the ant species it accepted seems to appear in anting literature, with the exception only of *Tapinoma sessile*, noted by Van Tyne (1943), and *Tapinoma* sp., by Ivor (1943; and in Nice, 1945). I find no mention of butyric acid or of the fact that a non-stinging, non-spraying ant species will induce anting. Thus far not enough attention has been given the various defense mechanisms among ant species used for anting; and even when the ant has been identified, its particular means of defense often has not been stated. Some writers seem to assume, quite erroneously, that all ant species used by birds have the ability to spray or that they all produce formic acid in quantity. Groskin (1950) believed that variations in birds' anting movements might be due to differences among ant species in aggressiveness and, he implies, in the composition of defense fluids. To this I would add difference in amount of the repugnatorial substance and in the method of ejaculation, *i. e.*, whether sprayed or exuded, for reasons that will be clarified later.

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TABLE 1

A Phylogenetic List of Ant Species Used by Birds for Anting

Ant nomenclature found in literature on anting is revised to conform to current usage. Insets under specific names indicate synonyms. This informal taxonomic synonymy follows Creighton, "Ants of N. Amer.," 1950, except for extra-limital species. Asterisk denotes species used by Orchard Oriole.

Subfamily and Species	Source
MYRMICINAE (Possess functional sting; other-	
wise do not eject repungatorial sub- stances)	
Monomorium pharaonis (Linnaeus)	(Den.) Poulsen, 1955, 1956; only by experienced Blue Jay
DOLICHODERINAE (Sting vestigial; exude repug-	
natorial liquid from anal glands)	
Iridomyrmex detectus (F. Smith)	(Austrl.) Bourke, 1941b; Galloway, 1948
*Iridomyrmex pruinosus analis (André)	(U.S.) Whitaker, this study
*Dorymyrmex pyramicus (Roger)	(U.S.) Whitaker, this study
*Tapinoma sessile (Say)	(U.S.) Van Tyne, 1943; Whitaker, this study
FORMICINAE (Sting vestigial; spray repugnatorial liquid from special formic acid gland; anal glands absent)	
Oecophylla smaragdina (Fabricius)	(India) Pillai, 1941; Ali, 1936, quoting H. Abdulali
Camponotus pennsylvanicus (DeGeer)	(Can.) Ivor, 1943
	(U.S.) Teale, 1953:168, of "car- penter ant"
Camponotus (Myrmophyma) innexus Forel	(Austrl.) Wheeler, 1951
Camponotus (Myrmobrachys) senex textor Forel	(Costa Rica) Skutch, 1948
Camponotus (Myrmepomis) consobrinus (Erichson)	(Austrl.) Chisholm, 1944; Wheeler, 1951
Lasius alienus americanus Emery	(U. S.) Dater, 1953
Lasius niger var. americanus	(U. S.) McAtee, 1944
Lasius niger (Linnaeus)	(Eng.) Carpenter, 1945; Longhurst, 1949
	(Switz.) Wackernagel, 1951
	(Den.) Poulsen, 1955, 1956
Lasius niger neoniger Emery	
Lasius niger var. neoniger (Emery)	(U. S.) Groskin, 1950
Lasius niger var. neoniger	(U.S.) Brackbill, 1948
Lasius niger	(Can.) Ivor, 1943
	(U.S.) Nice, 1945
Lasius (Dendrolasius) fuliginosus (Latreille) Lasius (Chthonolasius) mixtus (Nyl.)	(Ger.) Löhrl, 1952
Acanthomyops mixtus Nyl.	(Eng.) Hobby, 1946

TABLE 1 (Continued)

Lasius (Chthonolasius) umbratus aphidicola	
(Walsh)	
Lasius umbratus mixtus aphidicola	(U.S.) Brackbill, 1948
Acanthomyops claviger (Roger)	
Lasius (Acanthomyops) claviger (Roger)	(U. S.) Groskin, 1943, 1950
Lasius claviger	(U.S.) Davis, 1944
Acanthomyops interjectus (Mayr)	
Lasius interjectus Mayr	(U.S.) McAtee, 1938, quoting Kalm bach
Acanthomyops murphyi (Forel)	
Lasius (Acanthomyops) murphyi	(U.S.) Brackbill, 1948
Formica rufa Linnaeus	(Ger.) McAtee, 1938, citing Heine 1929
	(Eng.) Goodwin, 1951, 1952a, 1953
	(Switz.) Wackernagel, 1951
	(Den.) Poulsen, 1955, 1956
	(Neth.) IJzendoorn, 1952a, citin Abma, 1951
Formica obscuripes Forel	,
Formica rufa obscuripes Forel	(U.S.) Weber, 1935
Formica rufa	(U.S.) Nice and Ter Pelkwyk, 194
Formica exsectoides Forel	(,,-,-,,,,,,,,,,,,,,,,,,,,,,,,,,,
Formica exsectoides exsectoides (Linn.)	(U.S.) Staebler, 1942
Formica fusca Linnaeus	 (U. S.) McAtee (<i>in</i> Chamberlai: 1954), "probably"; Teale, 1953 159, 199
Formica fusca subsericea (Say)	(U. S.) Brown, 1953; Groskin, 194 1950; Nero, 1951; Brackbill, 1948 Hebard, 1949
Formica fusca var. subaenescens	(U.S.) Nichols, 1943, "probabl subaenescens"
Formica fusca s. sp. subaenescens Emery	(U.S.) Buell, 1945
Formica (Raptiformica) sanguinea Latreille	(Can.) Ivor, 1943, 1956
Formica (Raptiformica) subintegra Emery	······································
Formica sanguinea subintegra (Emery)	(U.S.) Groskin, 1950
cangannea caenneg.a (Innory)	

Methods

In summer experiments, I dug up entire ant colonies (earth, ants, pupae, larvae, eggs) and placed the material in a tray on the porch where the Orchard Oriole was free. Sometimes I confined the bird in a large, bottomless cage and placed the cage over the tray, or over an ant nest in the yard. Winter experiments were managed similarly indoors, with ants taken from captive colonies or, occasionally, from the yard. Spraying ants, unavailable locally, were never offered. Each experiment, except as otherwise noted, was made with a single colony. When more than one ant species was used in the experiment, all material of one species was removed before another species was offered. Duration of experiments varied from a few minutes to three hours, depending upon the bird's interest and the number of ant species offered.



FIG. 1. ((a) Orchard Oriole exposes undertail coverts in preparation for anting. Note ant in bill, and split web of an inner rectrix, caused by anting activity. (b) Bird apparently applies ant to both rectrices and remiges, shown interlocked. (c) Application to bases of outer rectrices. Note wing tip resting upon ground behind tail. (d) With tail pressed against folded wing, bird treats wing tip and possibly the ventral surface of tail. Note displaced (right) greater wing covert.

Lovie M. Whitaker

In three instances, two species of ants, readily distinguishable at sight, were mixed deliberately. In 1954 most summer observations were made with ants that daily invaded the porch in force, attracted by bird food. These invaders invariably appeared to be all of one species, and samples from them, taken July 30, were identified by Dr. Gregg as *Dorymyrmex pyramicus*.

The Orchard Oriole is trusting and permitted closest scrutiny, often performing 10 inches from my face. It never has been sick or injured. Examination with hand lens and brushing out its plumage disclosed no parasites. Since the first prenuptial molt, this female oriole has been in excellent condition, with bright plumage of normal texture and color. All subsequent molts have been autumnal. The bird's somewhat small size may be due to metabolic disturbances as a fledgling on a partly artificial diet.

PLUMAGE AREAS ANOINTED

Although observers do not agree, and reference to application to virtually every accessible plumage tract can be found in the literature, the wings and tail are almost always mentioned (see Adlersparre, 1936; Allsop, 1949; Brackbill, 1948; Chisholm, 1944; Fletcher, 1937; Goodwin, 1953*a*; Groskin, 1943, 1950; Heinroth, 1911*a*; Ivor, 1941, 1943, 1951, 1956; Nice, 1952; Osmaston, 1909, 1936; Reynolds, 1946; Tebbutt, 1946; Van Tyne, 1943; Wheeler, 1951, and others).

Ivor (1946, 1951, 1956) modified his earlier descriptions of applications to ventral surface of primaries by stating that ants are applied to the distal one-third of the primaries, rather than along their entire length; that apparently the undertail coverts sometimes are treated; and that the ventral surface of the tail is treated, although rarely. Poulsen (1955, 1956), however, said that his birds, excepting the Common Grackle (*Quiscalus quiscula*), applied ants only to the quill feathers.

My oriole regularly anointed the ventral surfaces of the outer few primaries, mostly near the tips. In doing this, the spread tail was brought sideward and forward; and the wing on that side was either folded or only slightly spread, with wrist lifted so that the wing tip was held *near* the basal section of the tail, or *against* the ventral surfaces of the rectrices (see Frontispiece). Application of ants caused wing tips to become frayed and their *dorsal* surfaces roughened by displacement of the barbs from beneath.

The ventral surface of the tail also was treated regularly, particularly the basal one-third (Fig. 1c). But it was the undertail coverts that seemed to be a main target. Here the deep, vigorous applications at times caused some of these yellow feathers to become so displaced as to stand up conspicuously above the olive-toned *upper* tail coverts!

Sometimes the bird treated its belly, and very occasionally the anterior crural feathers briefly. (For anting of the legs, see Brackbill, 1948; Hein-

TABLE 2 Ant Species Rejected by Orchard Oriole for Anting	
 Subfamily MYRMICINAE (Possess functional sting; otherwise do not eject repugnatorial substances)	
Pogonomyrmex barbatus (F. Smith) *Pheidole bicarinata buccalis Wheeler	
*Pheidole bicarinata longula Emery *Crematogaster (Acrocoelia) laeviuscula Mayr	

* Sting does not penetrate human skin.

roth, 1911a; Nice and Ter Pelkwyk, 1940; Snyder, 1941; Tebbutt, 1946; Troschütz, in Stresemann, 1935b.) The flanks and sides seemed to be touched only indirectly as the bird reached toward the wing tips and tail. The feathers of the sides and flanks became disarranged, but I could never detect direct, exclusive application to them. IJzendoorn (1952a), noting untidy, ruffled breast and abdomen of a Common Starling anting in the wild at high intensity, suspected the disarray indicated poor condition. The activity itself caused somewhat the same appearance at times in my oriole.

In the rare instances when the oriole applied ant larvae and pupae, it usually ate them afterward. Sometimes a larva or pupa was used when the bird applied the ant which carried it. On some days the bird ate directly eggs, larvae and pupae, yet often these were ignored. Burton (1955*a*) observed anointing with ant cocoons, the bird being a tame Rook (*Corvus fru*gilegus), which probably "at some time picked up an ant carrying a cocoon and now associates the two."

On a number of days I examined the oriole immediately after anting. I found ant odor on all these areas mentioned, but no odor on other plumage parts. The odor was always strongest on the undertail coverts and adjoining portions of rectrices. For example, on February 24, 1955, I tested the bird after it had anted at high intensity for 18 minutes with freshly dug ants and I found odor on tips of the primaries, on undertail coverts, basal twothirds of the tail, and on sides and flanks. The feathers of the fronts of the tibiae were faintly scented. Odor was strongest on the undertail coverts. Save sides and flanks, I had clearly seen the bird treat all these areas. I could detect no odor on other plumage areas and none on the wings, except on the distal one and one-half inches of the primaries. These were, be it remembered, non-spraying ants. Neither on this occasion nor on any other have I seen the bird apply ants to dorsal surfaces of wings, tail or body.

I find but three references to odorous plumage, all relating to birds that used spraying ants. Wackernagel (1951) said his tame Carrion Crow (Corvus corone) became so scented with Formica rufa that it was still odorous next day. The scent of Lasius fuliginosus on tame European Jays (Garrulus glandarius) was evident at a meter's distance (Löhrl, 1952, 1956). Mr. John A. Johnson (letter, Sept. 17, 1954), in Michigan, informs me that his tame, free-flying Common Crow, which has sought unidentified ants of its own volition during nine summers, subsequently reeks with odor to the degree that his own hands become scented from handling the bird. From his description, I judge this bird used spraying ant species. All spraying ants belong to the subfamily Formicinae (Table 1).

POSTURING, TRIPPING AND FALLING

The awkward posturing and strange acrobatics of the oriole were similar to those described for many small species. Always there was some deflection of the tail, even during low intensity anting. Usually the tail was brought sharply around to one side of the feet, or between them, so that the tip pointed forward and the dorsal surface lay largely on the floor. Often the bird stood on the tail with one or both feet, or briefly sat on it. It habitually tripped on its tail, at times falling sideward or backward. Sometimes it turned complete *forward* rolls. Ivor, Poulsen, Van Tyne, Groskin (1950), Adlersparre, Osmaston (1909), Nichols (1943), the Shackletons, Nice (1943), Löhrl (1956), and others have observed falling or tumbling in anting birds.

The higher its anting intensity, the more the oriole tripped and tumbled. I have seen it stand with the tail turned out to one side while it looked for the next ant; but usually it kept these odd positions only momentarily, and after tripping or falling, would right itself in a flash. All imbalance occurred in conjunction with interference of the tail with feet. Never did this bird lie down, press its breast to floor, sprawl with spread wings, or behave in any way that suggested passive anting.

Likewise, the oriole never permitted ants to crawl upon it, and would quickly pick off those that got on its toes, often flipping away others that came too close. There was no evidence that the bird ever deliberately deposited ants in or on the plumage. Three times only did I see single ants sticking to its plumage, on a rectrix. Examinations in the hand revealed no ants on the bird. However, the projected transparencies show that ants sometimes were rubbed off on the feathers. In one picture two ants may be distinguished on the ventral surface of rectrices, in another an ant is seen on the ventral surface of a primary. These ants appear to be flexed; one of them plainly is wedged between barbs.

The literature indicates that only a few small birds, such as Redwing (Turdus musicus), Song Thrush (T. philomelos), European Blackbird (T. merula), American Robin (T. migratorius), Catbird (Dumetella carolinensis), Common Starling, and Indigo Bunting (Passerina cyanea), sometimes allow ants to crawl upon them in numbers (Bates, 1937; Callegari, 1955; Floericke, 1911, and in Stresemann, 1935b; Groskin, 1950; Govan, 1954; Shackleton and Shackleton, 1947; Poulsen, 1956).

MANNER OF APPLYING ANTS

Observers often mention a stroking or preening action of the bill as ants are applied (Adlersparre; Goodwin, 1955b; Brackbill, 1948; Buell, 1945; Van Tyne, 1943; Ivor, 1943, 1956; Laskey, 1949; Wheeler, 1951, and others). This was not the case with the captive Orchard Oriole. It always applied ants in quick dabbings, rather than strokings. Moreover, there was also a peculiar motion of the head. As the bird, ant in bill, reached toward the area to be anointed, it moved its head from side to side, so rapidly that the effect was almost that of shuddering. While reaching for the plumage and during each dabbing, thrusting application, the bird vibrated its head in this manner. When performing in a clinging position on the cage wall, the oriole sometimes caught its bill in the hardware cloth as it tried to reach its tail, and the bill rattled loudly and rapidly between the wires. This action on quill feathers produced a rustling sound. Invariably ants were applied thus; but during low intensity anting, vibration and dabbing were likely to be shorter in duration and noticeably slower.

Though these head movements have not been described precisely heretofore, they probably occur in many birds. Adlersparre said only that two Orange Bishops (Euplectes franciscana) shook their heads so energetically they sometimes lost the ant from their bills. Poulsen (1956) stated that his birds would "rub the bill among the wing-feathers downward towards the tip with quivering movements of the head"; and he mentioned that they sometimes would shake their heads "more or less vigorously." Both of these writers seem to attribute this behavior to ant spray, a factor not present in the case of the oriole. In response to my query, Ivor (letter, February 16, 1955) wrote that he noticed, on that day, both the dabbing applications and vibrating head for the first time, in the case of a Baltimore Oriole (Icterus galbula); and, further, that he believes that, in working with groups of anting birds, he had previously overlooked these motions. Bourke (1941b) told of Rufous Whistlers (Pachycephala rufiventris) that took ants to bushes and there shook their heads from side to side a few times, then dropped the ants and preened. Head shaking preceding ant applications has been reported in Indian Mynahs (Acridotheres tristis), according to Chisholm (1944); and the Cockatoo observed by Glauert behaved similarly with an ant and again when tobacco juice got in its mouth.

Among numerous responses Ivor received, following his recent paper (1956), was one from Henry Petersilie in New York, suggesting that birds may fall over in "ecstasy" because of disturbance in the semicircular canals of the inner ear. The idea has merit. Granted a disturbance to balance mechanism, from head shaking or other cause, this alone would not seem enough to have caused the oriole's loss of footing; for the bird was not seen to trip or fall except when the tail was brought into contact with feet and legs. But

there remains the possibility that loss of balance through interference of the tail was augmented by some such condition.

TREATMENT OF ANTS

The captive Orchard Oriole seemed to roll these small ants excessively. Usually each one was worked in the bill, and apparently crushed, regardless of its ultimate disposition. Supplies of acceptable dead ants were treated in like manner. I could not tell how severely the bird damaged an ant before applying it; but ants that it had rolled and cast aside unused were so injured they could not crawl. Those flung away after application were either dead or severely injured. Examination of 14 such "used" ants under binocular microscope showed 13 with damaged gaster, several with tissues extruded. Some of them also had the pedicel, head or thorax injured and nearly all had lost appendages.

The bird habitually made several applications, each consisting of many tremulous dabs, with a single ant. Between applications, it would hesitate and roll the ant further. It seemed to me this was done in order to renew or increase the ant's effectiveness.

A number of records show squeezing or crushing of the ants (Troschütz, in Stresemann, 1935b; Ali, 1936; Nice and Ter Pelkwyk, 1940; Galloway, 1948; Poulsen, 1955, 1956; Teale, 1953:168) or that dead and injured ants were left on the anting grounds. Ivor (letters, February 1 and 14, 1955) and Teale (loc. cit.) each have noticed that workers of the large spraying ant (Camponotus pennsylvanicus) sometimes seem not to be crushed before being applied. Teale, Groskin (1950) and others have suggested that spraying ants may give off acid merely by being held in the plumage. Perhaps a bird's treatment of the ant may depend more upon the ant's spraying ability than upon its size. Formica rufa and its allies can eject a fine spray for a distance of 20 to 50 cm. (Wheeler, 1910:42-43). It should be recalled that my oriole used only non-spraying ants, and that crushing increased their odor. I found, however, in at least one of these species (Dorymyrmex pyramicus), that only the gaster seemed to produce odor. When the gaster was removed, crushing of the head, thorax and other parts did not seem to change or increase the ant's odor.

THE ANTING LOCALE

Birds have been observed anting in trees, on roofs or feeding tables wherever ants happened to be found. Sometimes they carry ants from ground to a tree or bush to apply them, whereas a captive bird may take them to its perch.

Usually my bird anted on the floor. Sometimes it performed on a perch, either bringing up ants or using those that crawled within reach. But it also had a habit of anting while clinging to the cage wall. It might fly to the wall with an ant and cling there to apply it, or hitch its way down the wall, snatch and apply an ant without touching the floor. At times the bird anted while clinging upside down on the wall—a position especially favorable for observing anointment of belly or undertail coverts. Skutch (1948) saw a Black Seed-eater (*Sporophila aurita*), anting in a bush, make one application while hanging upside down from a twig!

ATTACKS BY ANTS

Surprisingly few accounts show that anting birds are attacked by the ants or that they fear them, although some kinds used are formidable biters. Aside from Poulsen's Blue Jays (*Cyanocitta cristata*), which used a small species (*Monomorium pharaonis*), it appears that birds use only those ants incapable of stinging (Tables 1 and 2). Furthermore, Poulsen (1955, 1956) thought the Blue Jays' responses were due to conditioning. His birds in general rarely were cautions or hesitant in taking up ants; and, when bitten, would shake their legs, jump or pick off the ant and fling it away.

Groskin (1950) saw a Song Sparrow (*Melospiza melodia*) suddenly jump and dance around before resuming anting; Ivor (1943) said "numerous times it was evident an ant had bitten a bird"; Bourke (1941b) commented on the hastiness with which Rufous Whistlers removed ants gripping their feet; Wackernagel's Carrion Crow at times "showed severe fright reactions and jumped into the air, probably when bitten"; and Löhrl (1952, 1956) described similar behavior for this crow. Goodwin (1952a) noted fear and hesitation in Lanceolated Jay (*Garrulus lanceolatus*) and Beechey's Jay (*Cissolopha beecheii*) but not in some other species which apparently used the same ant species. These jays would first take ants to perches to apply them before anting on the ground near the ants.

My oriole approached the unacceptable *Pogonomyrmex barbatus* readily, yet carefully; but it showed no fear of other ants, except, as will be seen, with an acceptable species foraging *en masse*. True, throughout the period of study, the bird performed at times on wall or perch; but it seemed to fly up with an ant in quite the same way it carried off a grasshopper to be eaten. Moreover, with supplies of dead ants the bird behaved this way. Although it would pick up unacceptable ants, even eat certain species of them, I never saw it carry an unacceptable species from the floor.

On June 30, 1954, I discovered a file of ants reaching from the porch door to a screened section occupied by the Magpie. The ants came in force almost daily until September 30, and during this period I put the oriole with them at least once a week. As previously mentioned, probably all of these ants were *Dorymyrmex pyramicus*.

On July 8, after eight successive days of anting with these invaders, the oriole began performing mostly on perch or wall. In the following three

weeks, it showed increasing reluctance to perform on the floor. On July 12, 16, and 24, *all* anting took place above the floor. Yet, on July 31 and August 1, the bird anted only on the floor. This erratic behavior strongly suggested fear of attack. Probably the bird had been bitten at one of the times when it had been allowed to remain with ants after the observation period. Later, on August 3, I witnessed an attack that was to affect its performance for quite some time.

As I watched the oriole ant, it suddenly jumped straight upward and then began to probe between a middle and outer toe. Almost at once it flew to a perch and began probing gently at the spot. For several minutes it remained there quietly, looking somewhat subdued, now and then peering down at its toes. Presently it began performing with ants taken from the wall; but not again that day did it go to the floor, except once to snatch an ant and fly with it to a perch. During the following two weeks I tried the oriole with invading ants on seven days. Each day the bird anted, but only above the floor, although on each of two days it did perform a single anting on the floor.

GATHERING AND APPLYING WADS OF ANTS

Sometimes the oriole gathered a ball of ants in the bill tip and held it for a while before eating the wad, applying it, or flinging it away. Once, when anting interest was very low, the bird held a wad of ants for almost two minutes while sitting still on a perch. One or several wads were gathered on 14 days, including experiments with dead ants. I once counted 18 ants taken up in rapid succession. Some wads were larger. The ants, clinging to one another like filings to a magnet, were so injured they did not separate after being cast away. When a wad was applied, parts of it dropped off and the bird seemed to eat the remainder. Of unacceptable ants, only the *Pheidole* were gathered, and then eaten.

Not very many anting species have been reported to gather ants. The Blue Jay, observed by Buell (1945), evidently applied small masses of ants. Gough (1947) watched Song Thrushes apply one or two ants at a time but not the large numbers which some of the birds collected. Ringleben (in Stresemann, 1935b) did not make clear whether his Carrion Crow made use of the wad of ants before throwing it aside. Scheidler (in Stresemann, 1936) and Ivor (1956) mentioned captive Common Starlings filling their bills with ants and then rubbing them on the plumage. Gengler's (1925) captive Common Starlings and Funke's (1912; and in Stresemann, 1935b) tame Magpie used several ants at a time. Simmons refers to this behavior in these last two species, as do Goodwin (1955a; 1955b) and Löhrl (1956) to the Starling. Poulsen (1956) said that the Blue Jay and Common Starling often retained ants after applying them and that, by the process of applying and then retaining ants, these birds collected as many as 20 ants before discard-

ing or swallowing the mass. On one occasion he saw this in the American Robin.

REACTION TO ANT-NEST EARTH

A strange activity of the Orchard Oriole concerned not the ants themselves but their nests. On seven days, winter and summer, the bird ate particular bits of nest earth, taking soil only from one or two minute spots in the tray. It always seemed to examine the dirt very closely before finding a spot to its liking. At times I could see what appeared to be grains of earth on its long tongue. Once, after several daily anting sessions, the bird was surfeited and would not ant—yet it ate a little of the nest earth. On two days, with the unacceptable *Pheidole bicarinata buccalis* and *Pogonomyrmex barbatus*, it ate nest earth. Ants, eggs, larvae, pupae were not involved in these feedings, though the bird may have been finding infinitesimal pellets of food residue ejected from the ants' infrabuccal pockets or, conceivably, minute myrmecophilus arthropods (Wheeler, 1910:32, 378–397).

On February 24, 1955, I tested the bird with earth (free of ants) from a nest in the formicarium. The oriole ate certain bits of the earth; yet when I replaced this with garden dirt, the bird hunted over the tray but did not once touch bill to the soil. Next I gave it still another sample of formicarium earth. Again the bird ate soil particles. Twenty minutes later it anted at high intensity with ants fresh from the yard, but it ate no dirt.

I have seen no record of such feeding. Gravel was always available to the bird; and powdery soil, which it spurned for dust-bathing, it never ate. It is a guess that the oriole ate only soil particles impregnated with ant exudations, possibly soil that had lined brood chambers. Wheeler (1910:395) stated that galleries of populous ant colonies becomes "greasy from the attrition of the constantly passing ants." Ivor (letter, May 10, 1956) suggested that the oriole may have found some kind of beneficial mold in the nest earth.

FREQUENCY OF ANTING EPISODES

Little is known concerning frequency of anting in the individual bird. Groskin (1950) observed a banded Song Sparrow, probably two individuals, anting on five days during one month, often "several times a day"; and Mayr (1948) saw a Song Sparrow ant almost daily in July in a certain stand of dock (*Rumex*) frequented by ants. Three Indigo Buntings in the wild used ants on four consecutive days (Shackleton and Shackleton, 1947). John A. Johnson (letter, September 17, 1954) advised me that his tame Common Crow ants perhaps once a month or whenever the weather is warm and dry. Goodwin (1951) found his six European Jays would not ant "two or three days running" and that a week or more seemed necessary between sessions for "keen" performance. Ivor (1951:177) believed his birds would ant only occasionally if ants were kept in the aviary.

Lovie M. Whitaker

On the other hand, Poulsen (1956) stated: "Many birds eating and anting with ants did so every day—sometimes several times daily—for more than a month." But he found that some of the species which applied ants but also allowed ants to invade their plumage (*Turdus philomelos* and *T. musicus*) did not respond again until three days later, while an American Robin, having refused to ant for three consecutive days, anted on the fourth day.

Study of individual differences in amount of anting is long overdue. Why, among captive Magpies (*Pica pica*), should one bird ant and the others never ant? Why did Goodwin's (1955b) Lanceolated Jays ant at their first opportunity, in 1951, and thereafter refuse? Why did some of Ivor's (letter, November 25, 1955) anting birds, among them individuals that had anted for years, either refuse or ant only sparingly during repeated tests in spring, summer and fall of 1955?

These and most references to frequency of anting or to absence of anting in experimental birds are unsatisfactory in that there are no precise statements on the quantities of ants supplied, and often the ants have not been identified. Poulsen (1956) gave his birds "a shovelful of earth containing several ants." Sometimes my oriole ate many ants before beginning to apply them. Thus, a bird given a limited daily supply might be expected to show a different frequency of anting from that occurring when its supply is abundant enough to permit daily surfeit. I believe that the amount of insect food in the diet of a captive bird also may affect anting responses, and that a captive starved for fresh insects may eat all of a limited supply of ants without performing any anting.

In this connection, I should emphasize that whenever the oriole had access to invading ants (see Methods) these were in almost limitless supply and continued to invade long after the bird had lost all interest in them. Also, in a majority of the other experiments more ants were offered than the bird could use.

I found anting frequency was high in my oriole, at least in summer. In 1954, between June 30 and September 19, the bird was put with invading ants on 41 days. Of these 41 days when there was opportunity to ant with the same species of ants in their natural state, the bird performed on 34 days. On three other days there was circumstantial evidence of anting; for, on these days, I did not remain to watch the bird, yet later I found scores of dead ants on the floor. On only four days did the bird refuse to ant.

In July alone, during 24 contact days with these ants, the oriole anted on 19, gave circumstantial evidence on three others (the three days mentioned above), and refused to ant on only two days. Also, on three of the 19 days (July 5, 8, 9) the bird was placed with the ants both morning and afternoon, and it anted each time.

The longest period of successive daily performance by the oriole was 10

days (June 30 to July 9); the next longest was seven days (July 31 to August 6). Both sequences occurred with invading ants.

For the entire 31-month study period (March 23, 1953, to October 6, 1955), negative response was even lower. Out of 77 contact days (not including the three days of circumstantial anting), the oriole's response was positive on 67 days and negative on 10 days. Analysis of the 10 refusals shows that the bird refused because of apparent surfeit on only four days. On the other six days rejection was due either to the presence of strangers (one day, with acceptable ants available) or to the fact that only an unacceptable ant species had been offered (five days).

DURATION OF ANTING EPISODES

Anting birds frequently perform from a few minutes to one-half hour. Two Scarlet Tanagers (*Piranga olivacea*) anted, with short interruptions, for more than one hour (Groskin, 1943); three American Robins anted in turn for over 45 minutes (Nichols, 1943); and a Common Grackle used green fruits of *Magnolia acuminata* for over an hour (Parks, 1945). In the case of three Cardinals (*Cardinalis cardinalis*) observed by Kurata (Snyder, 1941) to ant for about two and one-half hours, it is not clear whether the birds were under continuous observation or that this constituted a single episode.

My oriole commonly anted for 25 minutes; that is, from the time it began to apply ants until the time it quit or the ants were removed. Frequently it performed for 45 minutes and was still anting when I ended the experiment. On May 22, 1954, the bird anted for 19 minutes with dead ants, and soon thereafter, for 30 minutes with live ants. Again, on April 3, 1954, during one hour and 55 minutes, when the bird was given three separate and varying supplies of ants, it performed for 3, 13 and 20 minutes, in that order. Winter sessions at times were equally long. On January 14, 1955, the oriole anted intermittently for about 90 minutes while Dr. A. A. Allen was taking pictures. Two weeks later it anted for 45 minutes, when there had been no unusual distractions.

As a rule anting continued quite steadily, with brief intervals now and then when the bird might search for ants, rest, or engage in unrelated activities. When anting at top intensity, the bird applied ants, one after the other, as fast as it could snatch and use them. But after a few minutes of such rapid action, it would stop anting and stand still for a while, as if exhausted, before resuming. I was impressed by the bird's strenuous, apparently compulsive, exertion. During warm weather, in strong sunshine, it sometimes stood and panted, but its non-anting companion, the Painted Bunting, did not react in this manner. After long, vigorous sessions, the oriole would feed and then sit quietly for as long as 45 minutes, sometimes sleeping. Ringleben (in Stresemann, 1935b), who stated that his Carrion Crow obviously was



FIG. 2. (a) Orchard Oriole, resting after anting, reveals displaced plumage of belly and side. (b) With one ant wedged in the left outer rectrix (showing below inner toe), bird reaches for another ant. (c) Oriole, ant in bill, almost doubles body in reaching toward juxtaposed wing and tail. Note open eyes. (d) Bird resumes normal pose after applying ant, still held in bill. Note lumps of earth thrown upward by motion of tail.

tired after anting for about 25 minutes, appears to be the only other observer who has noted fatigue.

SELECTIVITY IN THE ANTING BIRD

Goodwin (1951:621-623) said of captive European Jays, regularly anting with, but never actually applying, *Formica rufa*: "Attempts to induce anting with small numbers of other species of ants have failed, possibly because they were not offered in sufficient quantity." But he does not name the ant species. I found that the oriole would respond to few ants or to one ant. Adlersparre (1936), Nice (1943, 1955*a*), Nice and Ter Pelkwyk (1940), all had the same experience with actively anting birds of several species. Thus it seems that release of anting response in birds that apply ants is not dependent upon the quantity of ants. Certainly my bird consistently rejected abundant but unacceptable ant species, including harmless ones which it often ate. But I believe the quantity of ants can affect intensity of the performance. Anting in the oriole began at low intensity, as a rule, soon built to a peak, and continued in long plateau before gradually subsiding.

I never saw my bird use a substitute. Daily it fed on apple and orange, both of which are known substitutes (Hampe, in Stresemann, 1935b; Chisholm, 1944; Laskey, 1948; Nice, 1952). Hampe (*loc. cit.*) and Poulsen (1955) both reported that vinegar induced anting. But when I once put vinegar solution in the oriole's honey-water vial, the bird seemed puzzled. Three times it plunged the bill into the liquid, backing off as if in surprise and shaking its head. This bird also avoided burning cigarettes and fled their smoke. Fifteen wiggling, inch-long larval centipedes (Chilopoda) excited the bird but it would not approach them. After I had crushed the heads of several, the oriole took one but soon tossed it away.

Certain species, even individual birds, have used ants and one or more substitutes (Adlersparre, 1936; Poulsen, 1955, 1956; Burton, 1955a, 1955b; Nice, 1955a; Nice and Ter Pelkwyk, 1940; Scheidler, in Stresemann, 1936; Alvarez del Toro, MS). Dr. Alvarez found the Streak-backed Oriole (*Icterus pustulatus*) in nature using a species of small wasp, as well as two species of ants. Burton's astonishing Rook used ants, both burning and hot (but extinguished) cigarettes and matches, and small live embers, besides performing the same movements of anting whenever it could get within reach of smoke. This Rook, according to its former owner, reacted similarly to steam from an electric kettle, even knocking off the lid at times in order to reach the steam. A number of times it performed in front of an electric heater, apparently stimulated by the heat. But Burton's European Jay, though responding to snubbed but still warm cigarettes or blown-out but smoking matches, refused to use the unidentified ants, cold tobacco and the several other common substitutes offered it. Dr. P. H. Fluck (1948), whose tame Blue Jay used various bitter, sour fruit juices and hair tonic, informed me (letter, March 24, 1956) that he has a second such bird that anoints *only* with the hair tonic.

Poulsen (1956) noticed that anting in the Magpie-Robin (Copsychus saularis), Shama Thrush (C. malabaricus), Peking Robin (Leiothrix lutea), and Common Starling was more pronounced with Formica rufa than with Lasius niger. He pointed out that this last ant is smaller, weaker in its bite, and produces less spray. His Western White-Eyes (Zosterops palpebrosa) and Blue Sugarbirds (Dacnis cayana), on the contrary, were much more likely to perform with this smaller ant and were cautious with the larger species and rarely used it. In his opinion, all of this appeared to indicate that bird species differ in their sensitivity to the bite and spray of ants. One might mention that this also was a case of the smaller birds showing preference for the smaller of two spraying ant species.

My exploratory experiments with selectivity in the oriole yielded some interesting results. Whenever I offered either of the *Pheidole* forms, the bird usually ate them sporadically but never applied any of them. Yet immediately thereafter, it would ant at length with *Dorymyrmex pyramicus*. At the very first experience with *Pogonomyrmex barbatus*, the oriole seemed to sense its harmfulness. Always the bird handled this species gingerly, taking up the ant with a pick-flick motion that sent it tossing. When repeated treatment had stunned the ant sufficiently, the bird would pinch it slowly a few times before discarding it. On one occasion pinching either brought out a distasteful flavor, or the bird was stung; because suddenly the bird flung the ant aside and began working its tongue, shaking its head and repeatedly wiping the bill on the window sill where it had been standing. Never did the oriole eat or apply this species, although immediately afterward it would do so with acceptable ant species.

The ant *Crematogaster laeviuscula* was completely ignored. Indeed the only time I saw the bird touch an ant of this species was when I offered them from the hand and then they were thrown away at once. In the summer of 1955, this species, not *Dorymyrmex pyramicus* as in the previous summer, invaded the porch almost daily from mid-July to mid-August. The oriole was put with these ants a number of times; but, as far as I could determine, this species was rejected, both initially and repeatedly, without as much as an incipient peck. Since the bird seemed to enjoy killing the aggressive *Pogonomyrmex*, whose sting and bite both presented threats, it seems unlikely that the weak sting of *Crematogaster* was the deterrent. In any case, neither of these two ants is particularly odorous, even when crushed.

In addition to the four above-mentioned ants, the oriole also rejected a color variety of an otherwise acceptable species. This happened with *Dory-myrmex pyramicus*, an ant that occurred in my yard in two color varieties,

one blackish, the other pale amber. On June 21, 1954, I offered a nest of the amber-colored ants. The oriole looked them over casually but would not touch them, or the larvae and pupae, during 15 minutes. It did, however, once eat a bit of the nest-earth. I then added a nest (no larvae or pupae) of the readily distinguishable dark-colored ants. As I poured out these ants, the oriole was instantly alert, crouching and leaning out on its perch, as if in interested recognition. As soon as my hands were out of the way, it began to ant. But not once, during about 20 minutes of anting, did I see the bird take up a light-colored ant. Each time it chose a dark ant from the mixed colonies. (Specimens from both colonies, taken at the time, were identified by Dr. Gregg.) Three days later I brought in from the original nest site the remnant population of light-colored ants. Again, the bird refused to touch them. Regrettably, I did not test flavor and odor in these ants, and I never again found this pale variety.

Was rejection due to color? Or might the pale ants have been callows and thus less strong in odor and related qualities? According to Wheeler (1910: 534), the young worker ant first develops its own individual odor during the period when the integument is hardening and taking on adult coloration. Fielde (1905) has shown that a worker ant's individual odor intensifies or changes with age "to such a degree that they may be said to attain a new odor every two or three months" and that hostility between colonies of the same species and variety may be caused by a difference in odor "coincident with difference in the age of the colonies." Morley (1941–1942) said that Fielde's work seems to show that ant odor is not fully developed until some time after callow stage and the ant is fully adult. Not recognizing at the time that age of ants might be of possible significance in anting, I did not preserve the pale specimens, once they had been identified.

A thorough study of selectivity needs to be made. No one knows precisely how or why birds make their choices of ant species or substitutes, or whether conditioning on a particular anting material actually occurs. Various non-anting responses of birds, some of them known anting species, to wasps (Hindwood, 1955; Goodwin, 1952b; Chisholm, 1952; Moreau, 1942; Rankin, 1950; Powne *et al.*, 1951), together with other cases of definite anting with wasps (Alvarez del Toro, MS; Freitag, 1935; Butler, 1910), suggest that birds may be similarly sensitive to differences in wasp species, in some of which *both* sexes are stingless. Butler (*op. cit.*) said, of *Garrulax* sp., only that "the wasp is seized and its tail rubbed backwards and forwards between the tail-feathers of the bird, either in order to break the sting or exhaust its venom before it is eaten."

REACTION TO DEAD ANTS

Both stunned carpenter ants (*Camponotus* sp.) and dormant ones have been applied by various small birds (Nice, 1943:81; Ivor, 1943, 1956). Of

dead "wood ants" (apparently some of them killed in test tubes in boiling water), Adlersparre said only that these ants caused his birds to perform as if with living ones.

On April 3, 1954, I placed 40 *Dorymyrmex pyramicus* on a metal tray, passed it momentarily over low heat to kill the ants, and offered it to the oriole. The bird came at once and ate two ants. Its manner was casual and, during 10 minutes, it applied but four ants, two of which were afterward eaten, and ate 10 others directly. The dabbing and vibrating movements of the bill were very much slower than usual. There was no tripping, and *only* the wing tips were treated. The actual anting span was about three minutes.

I then offered approximately one-half of the nest from which these ants had been taken, together with its living workers and larvae, but no pupae. Now the oriole anted for 13 minutes, using all ants that did not crawl out of reach. Anting intensity was high. Many ants were eaten, with and without application. Forty minutes later, I replenished the tray with the remaining portion of the nest. This time the bird anted at top intensity for 20 minutes, after which I removed the ants. It rolled, fell down and tripped; but it ate few ants and incapacitated ones littered the floor. The usual plumage areas were anointed; and I noted three applications to the crural tracts.

Substantially this same experiment was repeated seven weeks later, on May 22, when I offered first 50 heat-killed ants (probably the *Dorymyrmex*), and then their nest containing live ants and pupae. On this day response to heat-killed ants was somewhat more pronounced. The bird performed intermittently with dead ants for 19 minutes, but with a marked lack of eagerness. Again movements were slow, yet at least 13 applications were made to basal section of the tail (*once* to undertail coverts alone) and eight to wing tips. Eight dead ants were eaten before anting began. Most ants applied were afterward eaten, but I noted nine others were eaten directly. Again, live ants induced intense anting until they were removed after 30 minutes.

A third such experiment next day, with *Iridomyrmex pruinosus analis*, brought a different result. When 150 heat-killed specimens, together with eggs but no larvae or pupae, were offered, the bird refused to perform during 17 minutes. In the first 11 minutes the oriole expressed some interest and ate nine ants; then it hunted over the tray and floor as if seeking live ants, now and then probing at the dead ones without picking up any.

Ten minutes later, I tried the bird with 150 live ants from the same colony, placing them on the bare tray, along with a few eggs. Instantly the oriole was attentive. It ate three ants and then began to perform as usual but at moderate intensity, until only a few dead or maimed ants remained. Twentyfour minutes later I gave the bird the nest of this same colony with the remainder of its population, including eggs, larvae and pupae. The oriole ate four ants, then anted at moderate intensity for 15 minutes. On November 1, 1954, the oriole applied and ate the few dead, wet ants (probably the *Dorymyrmex*) offered it. These ants had drowned in a formicarium moat. Next day I offered on a saucer about one-half teaspoonful of drowned ants which had been dried at room temperature. There was quick interest, but the bird, unfamiliar with the saucer, seemed afraid. Twice it climbed down the cage wall until it could reach an ant, then applied the ant while clinging upside down. Thereafter the oriole anted readily on saucer and floor for 12 minutes. The usual areas were anointed, including the undertail coverts. When all ants had been "used," the bird hunted for more and applied discarded ants, some of which had been applied previously. Anting intensity was high. I counted 55 ants applied, some of which were afterward eaten, and a number eaten without previous application.

Frozen ants (probably the *Dorymyrmex*) from several colonies, collected in early November, 1954, and stored in a tight but not air-tight container, were also used by the oriole many times that winter through January 18, 1955. I had drowned, rinsed and drained the ants before freezing them. Whether few were offered or many dozens, the bird always performed. Given small numbers, the oriole usually ate each one, about half of them being first applied, and often it hunted for more. It used frozen ants with somewhat less enthusiasm than it exhibited with live ones, yet the usual plumage tracts were treated and action and interest usually were keen.

Then, on January 31, 1955, the bird ate 16 of approximately 100 frozen ants but it refused to ant during 13 minutes. Five minutes later it gave an average performance with live ants from the formicarium. By this time the frozen ants, stored over two months, had lost much of their odor and flavor, a significant change to be described later. Furthermore, frozen ants thereafter were eaten but never again applied, although the bird continued to perform with living ants.

REACTIONS TO SUBTLE VARIATIONS IN THE ACCEPTABLE ANT

Each ant species accepted by the Oriole has only a simple worker caste; and sexual forms never were offered the bird. Nevertheless, during anting sessions, many ants were rolled and flung aside without being applied. Occasionally the bird would then toss its head and wipe its bill as if the ant had been mildly disagreeable. But in the next moment, another ant of the same species and colony would be rolled and applied, while a third one might be rolled and dropped. Frequently the bird returned to such discarded ants, even wads of ants, picked them up, rolled and discarded them again, still without applying them.

It was Margaret Nice who stimulated me to taste ants. I crushed between the teeth and tasted many ants from the supplies given the oriole, testing every species offered.

ANTING IN BIRDS

Lovie M.

Whitaker

I found all of the acceptable species, fresh from the yard, usually were sweet at first and then they produced a mildly burning sensation on the tongue. Strangely, individuals of a colony varied—a few of them, although sweet, did *not* burn. I found also that odor among these ants varied. Usually they were strong-smelling when crushed between thumb and finger, but some individuals gave off little or no odor. Larvae and pupae were faintly sweet, but did not burn the tongue; nor did these have the butyric acid odor so characteristic of adult workers. (According to medical science, strongly irritating substances, such as mustard or formic acid, applied to the skin, can produce measurable amounts of heat, due to dilation of the capillaries. There-



FIG. 3. Greatly enlarged section of Fig. 2c, showing effects of vigorous anting in Orchard Oriole. Note (a) rents in four outer primaries caused by bill; (b) ant-nest earth (showing as white specks in photo) on bill just to left of ant, and adhering to edges of punctures in webbing; (c) unworn condition of plumage beyond disrupted area.

fore, I shall use the term *thermogenic* in referring to *any* kind of burning or warming quality in anting materials.)

In addition, the burning sensation produced by these freshly dug ants seemed to vary with the season, and more of them were likely to have high thermogenic value during summer than in winter. For instance, on February 24, 1955, when the oriole used freshly dug ants at high intensity, most of the ants I tasted burned moderately, although certain others burned strongly or

221

not at all. But later, on May 24, when the bird anted at top intensity, the ants were very strong in thermogenic property, so much so that a single ant was enough to burn the whole tip of my tongue, and only an occasional one did not burn. Furthermore, when I collected some of these ants, as the bird applied and cast them aside, I found most of them burned strongly, although others burned faintly or not at all.

Some of these discarded ants had been applied only once, and briefly. I suspected the bird was applying sparingly those ants which had little or no thermogenic property. I then collected and tasted, immediately after they were discarded, two additional ants which, I carefully noted, had been applied several times. Each of them burned my tongue excessively. O'Rourke (1950) discussed the variation in formic acid content of venom in several ant species. He mentions that Stumper (1922b) showed that temperature affected the rate of secretion in *Formica rufa* and that Stumper's results gave a Q^{10} of 2.16—that is, a rise of 10° C. increased the rate of secretion 2.16 times, or roughly doubled it.

Deterioration in the qualities of frozen ants was noted (p. 220) after several weeks of storage. On November 22, 1954, I could detect no change in ants stored since November 4; but by January 31, 1955, when the oriole refused frozen ants for the first time, I found them to be very much less sweet and odorous and to have *no* burning quality whatever. The changes probably had developed earlier, because, when the bird was given a small quantity of them on January 18, 1955, it ate all of them but applied only three. Of even more significance, it treated only the wing tips, once possibly touching the edge of the undertail coverts in doing so, and the right crural tract this last a plumage area not usually anointed.

I did not test the thermogenic property of heat-killed ants at the time of those experiments. However, it seems probable that the heat had been sufficient to lessen or destroy that property, thereby causing either poor anting response with slow action or outright rejection, as already described. Later, on October 20, 1955, when I did test the effects of heat, applied in the same way, on *Tapinoma sessile*, I found the thermogenic value was very much affected. Of 12 live *Tapinoma*, nine burned the tongue mildly to strongly, and three produced no burn whatever; whereas, of 12 heat-killed specimens from the same colony, nine gave no burn, while three burned slightly.

Unacceptable ant species differed markedly from acceptable ones in these respects. Neither the *Crematogaster*, the *Pogonomyrmex*, nor either of the *Pheidole* forms had appreciable odor, even when crushed. These species were all rather tasteless, not at all sweet, and they did *not* burn.

These variables within the ant colony seemed to explain why the oriole would eat one ant, apply the next, and fling a third away unused. I could not be sure, of course, whether the bird's reaction to a given individual was Lovie M. Whitaker

determined by that ant's sweetness, odor, heating quality, or by factors yet unknown. Evidence that the thermogenic property stimulated anting in the Orchard Oriole may be summarized thus:

1. All ant species accepted produce a burning sensation to the human tongue.

2. The four unacceptable ant forms were found to lack thermogenic property.

3. Larvae and pupae of acceptable species, lacking heating property, were rarely applied.

4. Ants of acceptable species, when subjected to heat that tended to destroy the thermogenic property, brought either very low or negative anting response.

5. Ants of acceptable species, when frozen, remained acceptable until prolonged storage had destroyed their thermogenic quality; once this change occurred, frozen ants were no longer accepted.

Since the general level of thermogenic property in the ant population appears to be lower in winter, it may very well be that the oriole's tendency toward somewhat milder anting response in winter was due to the condition of the ants themselves at that season. Ivor (1943) found the interest in anting pronouncedly lower among his birds in winter.

My fragmentary explorations into the properties of ants that appear to induce anting show the need for full study along this line, if we are to have thorough understanding of anting behavior. The oriole's selectivity also demonstrates that the behavior of birds in the presence of ants cannot be evaluated without determination of the ant species and variability within the colony. This is illustrated further by the instance of birds (several known anting species) congregating to feed on unidentified winged ants but not performing anting actions (Worth, 1938). In this connection it is significant that anting has not been recorded among birds following the purblind, noisome army ants (*Eciton*) of vestigial sting (Schneirla, 1956; Skutch, 1954: 24; Johnson, 1954; Sutton, 1951); and that Elliott (1950), describing relations of birds with red driver-ants, "probably . . . *Dorylus (anomma) nigricans*," did not mention anting.

Since birds are known to ant with beetles and bugs, anyone looking for evidence of anting among birds attending swarm-raids of army ants should bear in mind the possible role of the routed insects as anting materials. My Slate-colored Solitaire (*Myadestes unicolor*), for example, anoints itself with certain thermogenic beetles but not with some other beetles lacking that value, and thus far has rejected all ant species offered it.

Relation of Feeding to Anting

As I watched the oriole perform day after day, it became clear to me that this bird was not primarily interested in ants as food. For one thing, I soon noted that usually more ants were discarded, with or without application, than were eaten; and in some sessions few, if any, ants seemed to be eaten. For instance, on June 30, 1954, during 30 minutes of top intensity anting, the bird ate relatively few ants and I noted very few discarded without use. Yet afterward I counted 88 damaged ants on the floor before giving up the effort to make a full count. These, or most of them, were ants that had been applied. When ants were offered daily, the bird's anting interest tended to decline; and on some of those days, I did not see it eat any ants, although it continued to ant, however mildly.

On the other hand, when the bird's interest rose, following days of low intensity anting, I noted no corresponding increase in its intake of ants. On one such day the bird anted eagerly; but I could be certain of seeing it eat only three or four ants. Yet, while anting was in progress, I counted 56 incapacitated ants on the floor. Notes, made during periods when the bird was given ants on many successive days, contain several remarks that the bird's anting appetite was better sustained than its eating appetite.

No amount of anting seemed to allay the bird's hunger. When the oriole had access to its regular food, it sometimes ate during the anting session, and at times drank honey-water. After protracted anting sessions it commonly fed voraciously. When ants (probably *Dorymyrmex pyramicus*) sometimes were gathered with small grasshoppers in the collecting net, the oriole would apply them before turning its attention to the grasshoppers, which it relished.

Many anting records do not show whether birds were eating ants. Most of those that do note consumption of ants concern birds that performed active anting. Ivor (1941; 1943) said that his birds ate a majority of the ants they used. Poulsen (1955) stated that each ant was eaten, but that "the birds did not always make the anting movements before eating the ant"; and he later (1956) listed 19 species that were seen anting and sometimes discarding the ants. Goodwin (1952a; 1955b) said that some birds discard all worker ants after using them, and he described three species that habitually went through the motions of active anting without even picking up the ants. He (1955a) considered anting to be a "very distinct behaviour pattern, unconnected with feeding."

Curiously, Wackernagel's Carrion Crow, which apparently did not eat ants during the anting sessions, in one instance came back the next day to the anting ground and ate the dead ones that remained. Huth (1951) saw a Chaffinch (*Fringilla coelebs*) apply and then discard the ants. Stegmann (letter, April 10, 1956) observed that a Brown Dipper (*Cinclus pallasi*) in the Tien Shan Mountains, Siberia, in July, 1949, discarded the large brown ants. "Holding an ant in its bill, the bird would pass it over the feathers of the wings and of the sides of the body below the wings. This was performed with three ants, one after the other. The ants after being used were not eaten

ANTING IN BIRDS

Lovie M. Whitaker

but dropped anywhere." Chisholm (1944) saw no evidence of eating among a group of Common Starlings anting in the wild. He and others comment upon the numbers of incapacitated ants left on the anting grounds (see Brackbill, 1948; Thomas, 1941; Pillai, 1941; Wheeler, 1951).

It appears that birds performing passive anting usually do not eat ants during the act. This was true of at least five of the eight Common Crows and of the two Northwestern Crows (*Corvus caurinus*) for which I have been able to find records (Frazar, 1876; Weber, 1935, and letter, May 5, 1954; Ivor, 1951; John A. Johnson, letter, September 17, 1954; Frank L. Beebe, letter, March 15, 1954; and G. Douglas Morris, letter, November 25, 1956). Excepting one, these birds were all tame, most of them free-flying individuals.



FIG. 4. European Jay (*Garrulus glandarius*) in special passive anting posture. This species allows ants to invade plumage; it does not apply them, yet will make motions of picking up and applying ants to wings. Photographed by Dr. Hans Löhrl, Ludwigsburg, Germany.

The exception was the "gray-white" albinistic Common Crow which Morris (*loc. cit.*) saw anting beside a trail where many large black ants were crawling around a piece of rotten wood.

An investigation of the side effects of anting and ant consumption by birds would seem worthwhile. I have no explanation for the fact that my Orchard Oriole occasionally held a wad of ants in its bill for quite some time, but the behavior reminds one of the somewhat similar human use of ants as smelling salts (Butler, 1897; Löhrl, 1956). The ant Oecophylla smaragdina, used for anting, has been a regular food item among certain peoples in India, who, it is said, use it "against fatigue and the sun's heat" (E. H. A., 1889; Long, 1901). According to Dunglison (1846:334), Formica sp. "were formerly extolled as aphrodisiacs" and the chrysalides "are said to be diuretic and carminative. . . ." Gorsuch (1934) mentioned a quail that tried to save her nest from unidentified invading ants by eating ants "as fast as they approached until she died, possibly from formic acid poisoning."

PREENING AND BATHING FOLLOWING ANTING

The relationship of preening and bathing to anting remains obscure. The present meager literature on this aspect of anting suggests that preening and/or bathing after anting may prove to be pronounced only in birds that allow ants to crawl over them and in those birds that apply vegetable substitutes with the bill.

Simmons (1955), apparently making no distinction between types of anting, has generalized: "Normal preening and bathing are almost invariable sequels to anting." He sees in this the implication that anting functions in some way as a "superior preening method." However, Ivor (1943, and letter, April 7, 1956) has found both preening and bathing rare in his many species anting actively with ants. Wackernagel, Löhrl (1956) and Goodwin (1947; 1951) reported bathing following anting in certain species that permitted ants in their plumage.

Govan (1954) noted that her Rose-breasted Grosbeak (*Pheucticus ludovici*anus) bathed twice not very long after having anted in a skillet of sliced onions. And she described unusual bathing by a free-living Catbird that allowed ants to stream over its plumage during active anting. The bird indulged in five brief, successive periods of anting, between each of which it flew to a bath, where it crouched and turned about in the water, stroking its primaries with the bill and shedding ants into the water.

Wright (1909:340) observed a case of apparent anting soon *after* the bath, in a Blue-winged Warbler (*Vermivora pinus*) that dusted in a "black ant hill." (See Dater, 1953, for details on anting in this species.) The report on three Cardinals anting for about two and one-half hours and appearing wet at the end of that time seems to imply that the wetness was due to the ants (Snyder, 1941). The Shackletons (1947) described two anting Indigo Buntings whose tails and wings appeared wet, "as if drenched with liquid"; but they made no deductions. Perhaps these, too, were cases of birds anting after bathing, since there is nothing in these reports precluding the possibility. Here a note by Staebler (1942) seems significant. He and George M. Sutton, noticing the wet, disarranged plumage of an American Robin using *Formica exsectoides*, believed the bird was wet from bath or the heavy dew. My Orchard Oriole, normally enjoying one or more baths a day, usually had access to the bath during or immediately after anting; but its postanting baths were so irregular I did not keep full records. I did, however, make notes on 18 days when bath water was available. On seven days the bird bathed at once after anting, in one case first dozing about two minutes with head in scapulars. Excepting one day, these were sessions with live ants, and anting intensities were of top (two days), high (four days), low (one day) levels. The exceptional session was with drowned, air-dried ants, and anting intensity was high.

On five days the oriole waited from three to 15 minutes before bathing, once not bathing until it saw another bird do so. These performances, all with live ants, varied from top (three days), through high (one day), to moderate (one day) intensity.

On still another day, with live ants at high intensity, the oriole waited 30 minutes before bathing. On the remaining five days, the bird did not bathe during the ensuing hour, and once it sunned and preened at length instead. With one exception, these sessions were all with live ants and intensities were high (two days), moderate (two days), low (one day). Here the exception was with frozen ants, used at moderate intensity.

After my oriole's long and extremely exciting first experience with ants, it flew to a perch, fluttered and shook out its plumage, preened thoroughly, and then bathed. But I never again noted this exact procedure. In general, it seemed to me that bathing in this bird was too erratic to be attributed solely to the effect of ant substances on its plumage.

Although most anting records do not mention it, preening often has been reported in association with anting (Robien, in Stresemann, 1935b; Brackbill, 1948; Groff and Brackbill, 1946; Hill, 1946; Moltoni, 1948, and others). Yet, it must be pointed out, many of these instances involved use of substitutes or the invasion of the plumage by ants. Dr. Fluck wrote me that his Blue Jays, using substitutes, preened after anting, as was true of John A. Johnson's (MS) Common Crow following passive anting.

Aside from the preening that followed post-anting baths, preening in the oriole was highly irregular, both in occurrence and degree. Sometimes the bird preened not long after anting, often not at all or only much later. Occasionally it shook itself briefly, scratched its head or preened a little during breaks in protracted anting sessions. The bird did not concentrate attention on the plumage parts anointed and, except when preening was brief, it dressed the plumage as it normally would. It seemed to me that heat, fatigue and plumage displacement were certainly as important as the localized ant-ointment in motivating both bathing and preening in the oriole. I observed that handling of the bird, which caused exertion and roughened plumage, almost invariably induced preening, and oftimes rather prompt

bathing. Andrew (1956), studying toilet behavior of buntings (*Emberiza* spp.), stated: "Disarrangement of the body feathers often seems to provoke preening."

It appears that observers are overlooking the mechanical effects of anting. Close observation of my oriole showed that sustained anting resulted in disheveled plumage. Tripping and standing upon the tail often caused damage to rectrices. The dabbing action of the vibrating bill regularly roughened, and often split, webs at tips of the primaries. Damage to webbing, while not always conspicuous, was readily discernible. Figure 1a shows split web of a rectrix. Figure 3 reveals penetrations in the layered webs of the four folded outer primaries, and particles of ant-nest earth, transferred by the bill, adhering to margins of these openings in the web. Contour feathers never treated during anting sometimes were disarranged by the bird's falling and tumbling, as seen in Figure 2a. Extreme displacement of a greater wingcovert is shown in Figure 1d. The bird was photographed when in perfect plumage, following fall molt. Several published photographs of anting birds show split webs or the abrasive action of quill feathers pressing against the ground (Corby, 1950; Ivor, 1956; Löhrl, 1956; Poulsen, 1956). Yet these occurrences, as results of anting, have not been commented upon.

EXPRESSION OF THE EYES DURING ANTING

These non-spraying ants seemed to have had no effect whatever on the oriole's eyes. I found no unusual blinking, spreading of nictitating membrane, or peculiar stare in the oriole during anting, such as some observers report. The eyes seemed to close at the instant the ant was touched to the plumage, just as they close for deep preening. Photographs, taken a fraction of the second before (or after?) application and while the ant is almost but not quite touching the plumage, show the eyes open (Fig. 2c). Photographs taken when the ant was in contact with the plumage show that the eyes are closed or covered by the membrane (Fig. 1b and Frontispiece). Corby's (1950) photographs show two birds with eyes closed; one of them, with the ant held some distance from the plumage, suggests the ants were a spraying species.

I wonder whether the Mistle Thrush (*Turdus viscivorus*), opening and closing its eyelids (*palpebre*) while ants crawled in its plumage (Moltoni, 1948), and the Baltimore Oriole, photographed in anting posture with nictitating membrane filming the eyes (Ivor, 1956:113), may have been reacting to ant spray in their eyes, rather than expressing enjoyment or apparent rapture, as the observers interpreted. The ant (*Oecophylla smaragdina*), used by birds for anting, is said to cause smarting in the eyes of jungle people who crush masses of these insects for food (E. H. A., 1889).

When Goodwin's (1951) European Jays got acid of Formica rufa in their

Lovie M. Whitaker

eyes, they would close them instantly and hop away, to stand a moment as if pained. Various small birds, using *Formica sanguinea*, *Lasius niger* or *Camponotus pennsylvanicus* (all spraying species) partly closed their eyes just before application; but a tame Common Crow, while sitting among ants, "closed her eyes and remained quiet for minutes at a time" (Ivor, 1951). A tame Carrion Crow, applying and sitting among *Lasius niger* and *Formica rufa*, frequently drew the membrane over its eyes (Wackernagel, 1951). Löhrl (1956) said that Carrion Crows "often close their eyes with pleasure when they are lying in an ant hill." But Lühmann (1951) believed his four Carrion Crows closed their eyes to avoid ant spray. Poulsen's (1955, 1956) birds, of various species, applying these last two ant species, sometimes winked the nictitating membrane or closed their eyes, as was the case when they were sprayed about the head experimentally with certain acid solutions that induced anting movements. Sometimes they shook their heads or rubbed their eyes against their shoulders.

Simmons reported that his Peking Robins (*Leiothrix lutea*) shook their heads rapidly and leaped away when ant acid got into their eyes; and that in the Magpie (*Pica pica*) the membrane flicked across the eyes during anting as a protection against acid. But Govan stated that her Rose-breasted Grosbeak had a "trance-like stare" while using weevils found in oatmeal; and that another such bird, applying sliced onions, held the eyes "wide and expressionless," although afterward its eyes were misty and "almost shut."

ATTITUDES DURING ANTING

Forcefulness of the anting impulse and the apparent satisfaction derived from the act, whether active or passive, with ants or substitutes, are mentioned by numerous writers. The bird's attitude has been variously described as demonstrating enjoyment, excitement, purposefulness, or even apparent ecstasy and intoxication. An element of compulsion seems evident in the many cases where anting birds have ignored threat or refused to be distracted (Davis, 1944; Ivor, 1941, 1956; Groskin, 1950; Bourke, 1941b; Lewington, 1944; and others).

The strength of the anting drive also is seen in "displacement" anting and "anticipatory" anting (Armstrong, 1947:120; Goodwin, 1952*a*; Burton, 1955*b*, 1955*c*; Simmons, 1955; Poulsen, 1955, 1956; Laskey, 1949). According to Moynihan's (1955) definition, some of these anting acts may have been "redirection" activities.

In its first few encounters with ants, my oriole was tense and excited. During its initial contact, the bird erected its crown feathers, pulled up its body with feathers appressed, and held its tail high, as it stood among the swarming ants or ran rapidly about on the floor, snatching and applying them. Later on, there was an eager, deliberate tenacity in the bird's manner and
TABLE 3

A LIST OF BIRD SPECIES REPORTED TO ANT

Nomenclature is revised to conform with current usage. Arrangement of Passerine families and subfamilies follows Mayr and Greenway (1956). The list includes species using ants or substitutes, but not those using smoke alone. No attempt has been made to evaluate published records.

PHASIANIDAE	
Capercaillie (Tetrao urogallus)	Reymond, 1948
Black Grouse (Lyrurus tetrix)	Reymond, 1948
Ruffed Grouse (Bonasa umbellus)	Bump, et al., 1947:272
Scaled Quail (Callipepla squamata)	Thomas, 1957
Chukar (Alectoris graeca)	Reymond, 1948
Domestic Fowl (Gallus gallus)	Chisholm, 1944
Ring-necked Pheasant (Phasianus colchicus)	Teale, 1953:269; MS, quoting Dash- uta
MELEAGRIDIDAE	
Wild Turkey (<i>Meleagris gallopavo</i>)	Audubon, 1831:7; 1842:48; Sharp, 1914:65; McAtee, 1947, citing Sharp; Allen, 1946, citing Audu- bon
PSITTACIDAE	Les in a 1044 - Cl : 1 las 1044
Unidentified parrot	Lewington, 1944; Chisholm, 1944
$Cockatoo$ (Kakatoe sanguinea \times roseicapilla)	Glauert, 1947
Turquoise Parakeet (Neophema pulchella)	Chisholm, 1948:163–175
STRIGIDAE	M 1057
Horned Owl (Bubo virginianus) PICIDAE	Mowat, 1957
Wryneck (Jynx torquilla)	Stone, 1954
Flicker (Colaptes auratus)	
	F. M. Packard, MS
Green Woodpecker (Picus viridis)	Allsop, 1949; Stanford, 1949
Golden-fronted Woodpecker (Centurus	Alvarez del Toro, MS
aurifrons)	
DENDROCOLAPTIDAE Barred Woodhewer (Dendrocolaptes certhia)	Skutch, 1948
TYRANNIDAE	21 1 2 2 3
Ochre-bellied Flycatcher (Pipromorpha oleaginea)	Skutch, 1948
MOTACILLIDAE	
Tree Pipit (Anthus trivialis)	Poulsen, 1956
IRENIDAE	
Golden-fronted Leafbird (Chloropsis aurifrons)	Poulsen, 1956
Jerdon's Chloropsis (Chloropsis jerdoni)	Ali, 1936
Chloropsis sp.	Ringleben, in Stresemann, 1935b
LANIIDAE	
Bull-headed Shrike (Lanius bucephalus)	Kuroda, 1947, (of related behavior
	with meat)
BOMBYCILLIDAE	T 1043 1049 1054
Cedar Waxwing (Bombycilla cedrorum)	Ivor, 1941, 1943, 1956
CINCLIDAE	0 1050
European Dipper (Cinclus cinclus)	Creutz, 1952
Brown Dipper (Cinclus pallasi)	B. Stegmann, MS
Cinclus sp.	Heinroth, 1911a; Heinroth and Hein-
	roth, 1924-1932:32; Braun, 1924;
	in Gengler, 1925
MIMIDAE	
Common Mockingbird (Mimus polyglottos)	C. Hagar, MS; Levon Lee, MS
Common Catbird (Dumetella carolinensis)	Ivor, 1941, 1943, 1956; Thomas, 1946; Brackbill, 1948; Groskin, 1950; Brown, 1953; Govan, 1954

Lovie M. Whitaker

MUSCICAPIDAE

TURDINAE Magpie-Robin (Copsychus saularis) Shama Thrush (Copsychus malabaricus) Slate-colored Solitaire (Myadestes unicolor) Veery (Catharus fuscescens) Gray-cheeked Thrush (Catharus minimus) Olive backed Thrush (Catharus ustulatus) Hermit Thrush (Catharus guttatus) Wood Thrush (Hylocichla mustelina)

Ring Ouzel (Turdus torquatus) European Blackbird (Turdus merula)

Redwing (Turdus musicus)

Song Thrush (Turdus philomelos) (formerly T. ericetorum)

Mistle Thrush (Turdus viscivorus) Clay-colored Robin (Turdus grayi) American Robin (Turdus migratorius)

TIMALIINAE

Yellow-billed Scimitar-Babbler (Pomatorhinus schisticeps) Rusty-cheeked Scimitar-Babbler (Pomatorhinus erythrogenys) White-throated Laughing-Thrush (Garrulax albogularis) White-crested Laughing-Thrush (Garrulax leucolophus) Black-throated Laughing-Thrush (Garrulax chinensis) Gray-sided Laughing-Thrush (Garrulax caerulatus) Rufous-necked Laughing-Thrush (Garrulax ruficollis) Red-headed Laughing-Thrush (Garrulax erythrocephalus) Garrulax sp. Silver-eared Leiothrix (Leiothrix argentauris)

Peking Robin (Leiothrix lutea)

Poulsen, 1956 Poulsen, 1956 Whitaker, this study Ivor, 1941, 1943 Ivor, in Lane, 1951:177 Ivor, *in* Lane, 1951:177 Ivor, 1941, 1943 Ivor, 1941, 1943; Gr Groskin, 1949, 1950; Corby, 1950, and in Huxley, 1954 Reymond, 1948 Carpenter, 1945; Chisholm, 1948:163-175; Williams, 1944; 1947: Ivor, in Lane, 1951:175; Home, 1954; Tenison, 1954; Callegari, 1955 Troschütz, 1931, in Stresemann, 1935b; Ringleben, in Stresemann, 1935b; Poulsen, 1956 Bates, 1937; Chisholm, 1944; Gough, 1947; Wells, 1951; Fitter and Richardson, 1951; Kent, 1952; Poulsen, 1956 Abma, 1951; Moltoni, 1948 Alvarez del Toro, MS Ivor, 1941, 1943, 1951, 1956; Staebler, 1942; Nichols, 1943; Van Tyne, 1943; Davis, 1944; Law-rence, 1945; Brackbill, 1948; rence, 1945; Brackbill, 1948; Groskin, 1950; Corby, 1950, and in Huxley, 1954; Teale, 1953:158; Poulsen, 1956 Poulsen, 1956 Poulsen, 1956 Callegari, 1955 Poulsen, 1956 Callegari, 1955; Poulsen, 1956 Osmaston, 1909, 1936 Poulsen, 1956 Osmaston, 1909, 1936 Kleinschmidt, in Stresemann, 1935b; Butler, 1910 Poulsen, 1956; Goodwin, 1955b; Callegari, 1955 Troschütz, 1931, Stresemann, in 1935b; Adlersparre, 1936; Steini-

ger, 1937; Ivor, 1941, 1943, in Lane, 1951:175; Simmons, 1955;

TABLE 3 (Continued)

	Poulsen, 1956; Goodwin, 1955b; Callegari, 1955
Leiothrix sp.	Kleinschmidt, in Stresemann, 1935b; Lorenz, in Stresemann, 1936
Black-headed Sibia (Heterophasia capistrata)	Troschütz, in Stresemann, 1935b; Poulsen, 1956
Blue-winged Siva (Minla cyanouroptera) Yuhina (Yuhina nigrimentum) Yuhina sp.	Poulsen, 1956 Osmaston, 1909, 1936 Poulsen, 1956
PARADOXORNITHINAE Black-throated Paradoxornis (<i>Paradoxornis</i> gularis)	Poulsen, 1956
SYLVIINAE Golden-crowned Kinglet (<i>Regulus satrapa</i>)	Davis, 1939
MUSCICAPINAE White-bellied Cyornis (<i>Cyornis tickelliae</i>) Rufous-bellied Niltava (<i>Niltava sundara</i>)	Poulsen, 1956 Poulsen, 1956
PACHYCEPHALINAE Rufous Whistler (Pachycephala rufiventris) Little Shrike-Thrush (Colluricincla parvula)	Bourke, 1941 <i>a</i> , 1941 <i>b</i> Sedgwick, 1946
ZOSTEROPIDAE Western White-Eye (Zosterops palpebrosa)	Poulsen, 1956
MELIPHACIDAE Yellow-eared Honeyeater (<i>Meliphaga lewini</i>)	Bourke, 1941a
EMBERIZIDAE	
EMBERIZINAE Brazilian Cardinal (Paroaria capitata) Black Seedeater (Sporophila aurita) Red-eyed Towhee (Pipilo erythrophthalmus)	Poulsen, 1956 Skutch, 1948, 1954 Van Tyne, 1943; McAtee, 1944; Corby, 1950
Brown Towhee (Pipilo fuscus) Slate-colored Junco (Junco hyemalis) Harris Sparrow (Zonotrichia querula)	Paroni, 1954, (of an attempt) Ivor, 1941, 1943; Bagg, 1952 Ivor, 1943
White-crowned Sparrow (Zonotrichia leucophrys)	Ivor, 1941, 1943; Paroni, 1954
White-throated Sparrow (Zonotrichia albicollis)	Ivor, 1941, 1943; Teale, MS
Fox Sparrow (Passerella iliaca) Song Sparrow (Melospiza melodia)	Ivor, 1941, 1943 Nice and Ter Pelkwyk, 1940; Ivor, 1941, 1943; Nice, 1943; Mayr, 1948; Groskin, 1950
CARDINALINAE Common Cardinal (<i>Cardinalis cardinalis</i>)	Edwards, 1932; Ivor, 1941, 1943, 1956; Snyder, 1941; Sprunt and Chamberlain, 1949:510-511; Chamberlain, 1954, quoting Mc- Atee
Rose-breasted Grosbeak (Pheucticus ludovicianus)	Ivor, 1941, 1943, 1956; Govan, 1954
Black-headed Grosbeak (Pheucticus melanocephalus)	Ivor, 1943
(Pheucticus melanocephalus \times P. ludovicianus)	Ivor, MS
Buff-throated Saltator (Saltator maximus) Indigo Bunting (Passerina cyanea)	Skutch, 1948, 1954 Ivor, 1941, 1943; Shackleton and Shackleton, 1947; Poulsen, 1956
Lazuli Bunting (Passerina amoena)	Poulsen, 1956

Lovie M. Whitaker

FRINGILLIDAE

ESTRILDIDAE

PLOCEIDAE

PARULIDAE

ICTERIDAE

TABLE 3 (Continued)		
Orange-breasted Bunting (Passerina leclancherii)	Poulsen, 1956	
TANAGRINAE Superb Tanager (Calospiza fastuosa) Blue-breasted Tanager (Calospiza	Poulsen, 1956 Sick, 1957	
cyanoventris) Blue-necked Tanager (Calospiza cyanicollis) Scarlet Tanager (Piranga olivacea) Summer Tanager (Piranga rubra) Red-throated Ant-Tanager (Habia gutturalis)	Sick, 1957 Groskin, 1943, 1950 Thomas, 1941 Alvarez del Toro, MS	
COEREBINAE Blue Sugarbird (Dacnis cayana)	Poulsen, 1956	
ULIDAE Blue-winged Warbler (Vermivora pinus)	Wright, 1909; Dater, 1953	
RIDAE Brown-headed Cowbird (Molothrus ater) Boat-tailed Grackle (Cassidix mexicanus) Common Grackle (Quiscalus quiscula) (includes Q. q. stonei, Q. q. aeneus, Q. versicolor)	Nice, 1945; Hebard, 1949 W. W. Worthington, MS Ivor, 1941, 1956; Parks, 1945; Rob- inson, 1945; Groff and Brackbill, 1946; Hill, 1946; Brackbill, 1948; Laskey, 1948; Nice, 1952; Teale, 1952, 152, 152, 152, Brackbill, 1948;	
Tinkling Grackle (Quiscalus niger) Baltimore Oriole (Icterus galbula) Orchard Oriole (Icterus spurius) Troupial (Icterus jamacaü) Icterus sp.	1953:158, 170; Poulsen, 1956 Gosse, 1847:225 Ivor, 1941, 1943, 1956 Whitaker, this study; Ivor, MS Poulsen, 1956 Goodwin, 1953; Simmons, 1955	
Black-throated Oriole (Icterus gularis) Streak-backed Oriole (Icterus pustulatus) Red-winged Blackbird (Agelaius phoeniceus)	Alvarez del Toro, MS Alvarez del Toro, MS Nero, 1951; Teale, 1953:158; Poul- sen, 1956	
Common Meadowlark (Sturnella magna) Bobolink (Dolichonyx oryzivorus)	Ivor, MS Ivor, 1943; Nice, 1943	
FRINGILLINAE Hawfinch (Coccothraustes coccothraustes) Chaffinch (Fringilla coelebs)	Poulsen, 1956 Longhurst, 1949; Goodwin, 1951, 1955b; Huth, 1951; Poulsen, 1956	
Brambling (Fringilla montifringilla)	Poulsen, 1956	
CARDUELINAE Evening Grosbeak (Hesperiphona vespertina)	Ivor, 1941, 1956	
RILDIDAE Red-browed Waxbill (<i>Estrilda temporalis</i>)	Givens, 1945, (of smoke-bathing and attempted use of ants)	
CEIDAE Bubalornis (Bubalornis albirostris) House Sparrow (Passer domesticus)	Poulsen, 1956 Davis, 1945; Wheeler, 1951; Com- mon, 1956	
Chestnut Weaver (Ploceus rubiginosus) Yellow-shouldered Widow-Bird (Coliuspasser	Poulsen, 1956 Poulsen, 1956	
macrocercus) Whydah (Coliuspasser ardens) Long-tailed Widow-Bird (Diatropura progne) Jackson's Widow-Bird (Drepanoplectes jacksoni)	Poulsen, 1956 Poulsen, 1956 Poulsen, 1956	
Bengalese Finch (Munia striata), domestic	Ivor, MS	

jacksoni) Bengalese Finch (Munia striata), domestic form

TABLE 3 (Continued)	
Taha Bishop (Euplectes taha) Orange Bishop (Euplectes franciscana) Fire-crowned Bishop (Euplectes hordeaceus)	Adlersparre, 1936 Adlersparre, 1936; Poulsen, 1956 Poulsen, 1956
sturnidae Long-tailed Glossy Starling (Lamprotornis caudatus) Glossy Starling (Lamprotornis chalybaeus) Superb Starling (Spreo superbus) Rose-coloured Starling (Sturnus roseus) Common Starling (Sturnus vulgaris)	 Poulsen, 1956 Poulsen, 1956 Poulsen, 1956 Poulsen, 1956 OLD WORLD: Hoyningen-Huene, 1869; Heinroth, 1911a; Floericke, 1911; Gengler, 1925; Hampe, in Stresemann, 1935b; Moncrieff, 1935; Scheidler, in Stresemann, 1946; Creisholm, 1944, 1948; Gregory, 1946; Baggaley, 1946; Tebbutt, 1946; Gregory, 1946; Baggaley, 1946; Armstrong, 1947; 120; Prideaux, 1947, (of using smoke); Williams, 1947, (of using smoke); Williams, 1947, 1948; White, 1948, (of using smoke); Abma, 1951; Wheeler, 1951; Fitter and Richardson, 1951; Goodwin, 1952, quoting Binelli; Simmons, 1955; Poulsen, 1955, 1956 NEW WORLD: McAtee, 1938, quoting Kalmbach; Pearson, 1938; Brackbill, 1948; Ivor, in Lane, 1951:175; 1956;
Pied Starling (Sturnus contra) Indian Mynah (Acridotheres tristis)	Teale, 1953:158, 159, 199 Poulsen, 1956 Chisholm, 1935 <i>a</i> , 1944, 1948:163– 175; Pillai, 1941; Wheeler, 1951
Chinese Jungle Mynah (Acridotheres cristatellus) Indian Jungle Mynah (Acridotheres fuscus) Bank Mynah (Acridotheres ginginianus)	Poulsen, 1956 Poulsen, 1956 Poulsen, 1956
Indian Grackle (Gracula religiosa)	Poulsen, 1956
DICRURIDAE Drongo <i>Dicrurus</i> sp.	Fletcher, 1937
GRALLINIDAE Magpie-Lark (Grallina cyanoleuca) Apostle-Bird (Struthidea cinerea)	Chisholm, 1944; Galloway, 1948 Chisholm, 1944, 1948:163–175
CRACTICIDAE Australian Magpie (Gymnorhina dorsalis)	Sedgwick, 1947
ARADISAEIDAE Green Catbird (Ailuroedus crassirostris) Satin Bowerbird (Ptilonorhynchus violaceus)	Poulsen, 1956 Chisholm, 1944
CORVIDAE European Jay (Garrulus glandarius)	Robien, <i>in</i> Stresemann, 1935 <i>b</i> ; Hampe, <i>in</i> Stresemann, 1935 <i>b</i> ; Goodwin, 1947, 1951, 1952 <i>a</i> , 1953 <i>a</i> , 1953 <i>b</i> , 1955 <i>b</i> ; Löhrl, 1952, 1956; Simmons, 1955; Burton, 1955 <i>c</i> ; Poulsen, 1955, 1956

Lanceolated Jay (Garrulus lanceolatus)

TABLE 3 (Continued)

TABLE 5 (Continued)	
with	a, 1947, (of related behavior acorn: compare with Good- 1952a)
Ivor. 1943 MS; Davi 1952	tt, 1899:243; Ellicott, 1908; , 1941, 1943, 1946, 1956; Lane, ; Buell, 1945; Fluck, 1948 and ; Laskey, 1949; Corby, 1950; is, 1950; Miller, 1952; Anon., ;; Teale, 1953:158, 168; Nice, a; Poulsen, 1955, 1956
Beechey's Jay (Cissolopha beecheii) Goodw Green Magpie (Kitta chinensis) Goodw 1956	rin, 1952a, 1953a rin, 1953a, 1955b; Poulsen, 5
erythrorhyncha) sen,	/in, 1952a, 1953a, 1955b; Poul- 1956
Azure-winged Magpie (Cyanopica cyanus) Nonon 1955	niya, 1935; Goodwin, 1953a, 5b
Chis 1946	oth, 1911 <i>a</i> ; Funke, 1912; sholm, 1940, 1944; Reynolds, 5; Schierer, 1952; Goodwin, 5 <i>a</i> , 1955 <i>b</i> ; Simmons, 1955
	ton, 1909, 1936
Rook (Corvus frugilegus) Pridea M c smol	ux, 1947, (of using smoke); Meeking, 1949, (of using ke); Chappell, 1949; Good- 1953a, 1955b; Burton, 1955a,
Common Crow (Corvus brachyrhynchos) Frazar	, 1876; Weber, 1935; Ivor, in e, 1951:175–177
Northwestern Crow (Corvus caurinus) F. L.	Beebe, MS
Carrion Crow (Corvus corone) Heine,	1929; Laven, 1931; Ringle-
(Hooded Crow, C. corone cornix, included) ben, Sche Cone Well Wac	<i>in</i> Śtresemann, 1935 <i>b</i> ; srping, <i>in</i> Stresemann, 1936; dry, 1947; Coombs, 1947; ls, 1950; Lühmann, 1951; kernagel, 1951; Goodwin, <i>ia</i> , 1955 <i>b</i> ; Löhrl, 1956
Raven (Corvus corax) Jacobs	en, 1911

little or no excitement. Distractions sufficient to prevent or interrupt sunning, bathing or feeding rarely kept the oriole from anting. On a few occasions it called *chak*, but never sang during anting sessions.

SEASONAL FLUCTUATIONS IN ANTING RESPONSE

The Orchard Oriole performed in every month of the year. In the warmer months (March to August), when opportunities were most frequent, anting intensity ranged from top level to very low. In the periods from September to February it ranged from high to very low. Experiments did not test seasonal differences adequately, because of variation in conditions and species of ants offered. However, it is noteworthy that even live ants did not induce top intensity anting in September through February but did so from March through July. On the other hand, the oriole anted at high intensity in September and in November through February. As noted earlier, seasonal changes among the ants themselves appeared to affect intensity of anting response.

As would be expected, a breakdown of American and Canadian records of anting in the wild shows by far the greatest occurrence during May through October, with the highest incidence in August. I find no reports for December to March save in captive birds, except the North Carolina record of a Golden-crowned Kinglet (*Regulus satrapa*), using unknown anting objects in a tree in January (Davis, 1939). Captives appear to ant throughout the year. But Ivor, in Canada, seems to be the only observer who has given close attention to this feature. His birds, representing about 32 American and two or three exotic species, exhibited but little interest in ants except from late April through July.

It seems possible that winter anting may take place in the warmer parts of the United States, where ants are active above ground on sunny days. Observers in these regions should watch for the behavior. But, as Herbert L. Stoddard, Thomasville, Georgia, suggests to me, care should be taken that feeding on weed seed in the nests of harvester ants is not mistaken for anting.

There are relatively few records of anting from southern United States for any season, and only one conclusive record (Levon Lee, letter, May 13, 1956) from the area between western Texas and Oakland, California, as far as I have been able to discover. This lacuna in the Southwest, first noted by Kelso (1949), probably is more apparent than real, since several species breeding there are now known to ant (see Table 3). Because anting sometimes is inconspicuous (Nice, 1945), or resembles preening (Simmons, 1955, Poulsen, 1956), it no doubt often goes unrecognized. Jean Graber has called my attention to an unquestionable case of anting by a Cardinal reported as food-gathering (Edwards, 1932).

Considering how very little we know about anting, it might prove helpful if operators of banding stations would place ant colonies in the traps. Confined by water barrier, the captive colony requires little care and could be a means of obtaining valuable information, particularly as to general health and parasitism among birds anting in the natural state. Obviously ants chosen for this purpose must be of a known acceptable species.

Some workers dismiss all observations on captive birds, apparently because of such factors as inactivity, disease or unnatural diet. Others have been equally reluctant to accept reports of anting among free birds of groups long believed to be non-anting species, such as the Psittacidae or Picidae, simply because captives did not ant. These positions become untenable when we consider the many species, first known to ant in captivity, that are now known to ant in the same way in the wild, and *vice versa*. It may indeed be true that the captive bird is more prone to ant than is its counterpart in nature—lack of normal energy outlets alone might make the difference. But it remains to be demonstrated that captivity *per se* either causes or suppresses anting, or modifies characteristic anting patterns.

Anting in captive birds free of obvious ectoparasites has been reported by Poulsen, Adlersparre, Heinroth (1911a), Ivor (letter, May 5, 1954), Scheidler (in Stresemann, 1936), and others. Parks (1945) found no parasites on the Common Grackle he trapped immediately after anting. Beebe, Weber, and J. A. Johnson advised me that their several crows had no obvious ectoparasites, and Beebe adds that his birds had been dusted with a rotenone preparation prior to anting. Frazar's (1876) two Common Crows and the two or three Australian cases involving domestic fowl and free Starlings (*Sturnus vulgaris*), cited by Chisholm (1944), may be almost the only reports of anting in obviously infested birds. It is indeed interesting to see that an Old World oriole (*Oriolus melanocephala*), infested with mites, did not ant, although it ate the ants (Poulsen, 1956).

The plain fact of the matter is that we know almost nothing of the physical condition of anting birds. No one seems to have made skin scrapings or any close examination for minute ectoparasites. Endoparasites as a cause of anting have received scant attention. I have been unable to find a single instance of dissection study on an anting bird, yet at least two ants, one of them *Pheidole* sp., are known to be intermediate hosts for two types of cysticercoids in chickens (Jones and Horsfall, 1935; Eichler, 1936b). Since endoparasites may, through lack of intermediary hosts, be lost in the captive bird, they should be considered in connection with the onset of negative anting response sometimes seen in captives.

DISCUSSION: THE ANTING OBJECTIVE

Study of the anting pattern of the Orchard Oriole revealed that during intense anting, more often than not, the bird was dabbing ants in the region of the vent. The undertail coverts and very bases of the rectrices certainly were treated, if not the vent itself. As results of the bird's vigorous applications, I found that ant scent was strongest in this region and that the undertail coverts at times became mingled with uppertail coverts.

Tallies of applications indicated preferential treatment in that area also; however, these counts necessarily were incomplete because of the bird's rapid action and occasional obstruction of my view. One of many tallies showed 46 applications to basal half or less of tail, including 15 to the undertail coverts alone; and 22 applications to distal one-third or less of primaries, including a number wherein the basal part of the tail shared in the treatment, as will be explained.

Even when the wing tip was treated, it often seemed that the oriole really was aiming at the undertail region, and that the wing interfered. Almost invariably, as the bird began to reach back with the ant, it simultaneously tucked the posteror body down and under, until crissum at times touched the heels, and rectrices were brought forward on one side of, or between, the feet. In this latter posture, the bird sometimes would anoint the lower belly and the undertail coverts between its heels. Regardless of the area treated, the bird usually reached around on one side, bringing the tail around on that same side. In doing this, the wing on that side would be folded high upon the body, with remiges out of the way behind the tail (Fig. 1*a*). Or again, the folded wing might be held lower, along side and flank, so that wing tip lay against the ventral surface of the tail, as the tail was tucked under and pressed forward. This pressure of tail upon wing was strong (Frontispiece; Figs. 1*d* and 2*c*), and often caused rectrices to interlock with remiges (Fig. 1*b*). Though he does not discuss it, one of Löhrl's (1956) photographs of an anting Carrion Crow demonstrates a similar interlocking of wing and tail in a passively anting species. In much the same manner, some passively anting birds at times will apply ants with the bill, as his bird is shown doing.

During the oriole's treatment of the wing tip, when tail was pressing against it, basal parts of rectrices (including undertail coverts) at times received some of the anointment, thus increasing the proportion of applications affecting the undertail region. This situation is seen in the Frontispiece. The lacerated webs shown in Figure 3, together with the extreme displacement of undertail coverts, already described, indicate that the oriole's bill sometimes penetrated deeply into the plumage. All of this strongly suggests that, when anting in this tail-to-wing posture, the bird sometimes thrust the ant through the wing tip and onto the under surface of the tail. Certainly, at such times, I regularly noticed that the dabbing applications of the vibrating bill involved both the wing tip and the adjacent areas of the tail, including the undertail coverts. In several photographs of actively anting birds (Corby, 1950; and in Huxley, 1954; Poulsen, 1956; Ivor, 1956) this same juxtaposition (and wing-tail anointment?) is illustrated though unemphasized. However, Poulsen (op. cit.) did state that it "often looks as if" the tail is treated and that in some cases among starlings, weavers and babblers, he has seen the bill movements "proceed to the tail, which is held close to the wing."

This is not to say that the oriole never anointed the wing tip when the wing was slightly spread and held just clear of the body and tail. It did so regularly; but instead of holding the opened wing out to the side as some birds do, the position of the wing was like that assumed for stripping the outer primaries during preening. Furthermore, this posture was seen less often than either of the other two anting positions just described, and at such times the applications themselves often were atypical. That is, the dabbing action of the bill often was so slow or so brief as to give me the impression that the bird was anting "absent-mindedly"—or possibly confusing anting with preening. Frequently, when anting in this position, the bird would dab the ant about on the wing tip a time or two and then stop, as if confused.

Aberrant anting action was seen again in the oriole's occasional treatment of the crural tracts. Instead of dabbing forcefully, as it did in anointing other areas, the bird *always* would play the ant about on these feathers very lightly, briefly and, it seemed to me, ineffectually and sometimes accidentally. Ivor (1943) has described somewhat similar action in young Wood Thrushes (*Hylocichla mustelina*) that sometimes anted at breast, abdomen and flanks, without actually touching those parts; and Brackbill (1948) noted an American Robin that twice seemed to dab at, but not actually touch, its breast during anting. Poulsen (1956) mentioned that an Indigo Bunting, while applying ants, intermittently made incipient movements of picking up and applying an ant.

These unusual motions, as well as the oriole's sometimes odd wing treatment, might well betoken uncompleted anting acts, occurring when the individual ant used happened to have an inadequate amount of stimulant. Conclusive evidence might be obtained through controlled experiments with spraying ants which previously have been forced to substantial ejection of their defense fluid and then washed. It seems quite possible that such depleted ants could produce significant differences in a bird's anting actions. Poulsen (1956:281) noticed that "birds anted much less with ants [spraying species] which had been kept in a sack for some days and therefore were less active." (Might the rate of venom secretion in the glands of these apparently unfed captive ants have been lower?) My experience with the Orchard Oriole leads me to believe that more precise experimentation with heat-killed ants might show correlation between the level of thermogenic property in the ant and the plumage area treated. I suspected the oriole of using the more strongly stimulating ants on the undertail coverts and bases of rectrices.

It must not be supposed from the foregoing discussion that the oriole treated only the proximal half of the tail. Frequent anointment of the distal portion was extended at times to the very tips of rectrices. Commonly, however, an application to the distal part of the tail *began* as an application to undertail coverts or bases of outer rectrices, the bird merely continuing to reach and dab farther along the tail before stopping and straightening up.

The thermogenic property of ant species accepted by the oriole presumably is due to an irritant in the secretions of their anal glands. Ants of the subfamily Dolichoderinae, which includes all of the acceptable ant species studied here, are known to smear their defensive secretions on enemy ants with frequently fatal effect (Wheeler, 1910:45). It seems, however, that myrmecologists have not determined the irritating constituent in those ant species my bird used. The unpleasantly odorous butyric acid, which these ants are believed to produce in quantity, is non-caustic. A free acid in butter, it has been noted also in meat juice, perspiration and excrementa. It would be helpful to know whether all insects used for anting produce burning sensations. Ants producing formic acid in quantity no doubt do burn, since this is a strong caustic. Many birds have used ants of this type. It appears, therefore, that a sensation of heat is a probable factor in most anting situations, as Burton (1955c) surmised.

In speculating on causes of anting, it would be well to keep in mind these points: (a) the fact that a bird sometimes will persist despite interruptions and threat situations, or even continue anting to a state of obvious fatigue; (b) that in captives, at least, the amount of anting varies among species and among individuals of a species; (c) that sudden, unexplained, even apparently permanent abstinence has been seen in captives; (d) that not all captives of a species will ant; (e) that apparently not all, or even most, individuals of a species and passive anting are not necessarily mutually exclusive—some passively anting species exhibit elements of active anting, and *vice versa*; but among birds under 10 inches in length, passive anting elements seem to be unusual.

Gross ectoparasites as a cause of the oriole's pronounced anting of the undertail region would have to be ruled out. There was no evidence whatever of such parasitism. But it is possible that itch mites (Acarina) might have been present in skin of the vent and its environs, especially mites in the pockets at feather insertions. Tapeworms (Cestoda) or roundworms (Nematoda) emerging from the vent, or flukes (Trematoda), sometimes known to encyst beneath skin in that region, might possibly cause itching. (For discussion of parasites see Rothschild et al., 1952:39-242; Peters, 1930, 1933, 1936; Boyd, 1951; Eichler, 1936b.) Aside from attention given this area during anting, I saw nothing in the oriole's behavior suggestive of irritation. It did not pick, preen unduly or rub its posterior. Yet it did thrust ants among the bases of rectrices and, when treating the outermost few of them, was seen to apply ants at the feather insertions. (Also, if parasites were the sole cause of the bird's anting, then these must have been host-specific ones, for the oriole's companion, the Painted Bunting, has never anted.) There are many records of repeated applications to undertail coverts, "base" or "root" of tail; and in some other cases such treatment seems implied (Bates, 1937; Goodwin, 1953a; Groskin, 1950; Nice and Ter Pelkwyk, 1940; Osmaston, 1909, 1936; Thomas, 1946; Staebler, 1942; Snyder, 1941; Brackbill, 1948; Davis, 1950; Home, 1954; Tebbutt, 1946, and others.)

The pleasure principle, on the other hand, seems a more likely basis for theorizing on the oriole's behavior. If, as it appears, the bird's mouth parts are sensitive to thermogenic properties in ants, it seems reasonable to suppose the vent, and perhaps the skin of the undertail region, would be similarly sensitive. Indeed, Simmons suggests that the area of the vent must be a

ANTING IN BIRDS

most sensitive spot. Ant secretions might cause a peculiarly pleasurable sensation of warmth, possibly with an element of the masturbatory in it. Autoeroticism is known in domestic parakeets, and, according to Armstrong (1947:160), also in parrots, ruffs, avocets, sage grouse and penguins. One wonders whether the posture of Carrion Crow on its perch, after having anted on the ground, could be a result of heat, fatigue, mild sexual stimulation, or



FIG. 5. Carrion Crow (*Corvus corone*) in ordinary passive anting posture typical of certain larger corvids. Note spread tail, somewhat pulled toward left wing, and lifted contour plumage. Photographed by Dr. Hans Löhrl, Ludwigsburg, Germany.

some combination. Goodwin (1953a; 1955b, figure) showed the bird in relaxed attitude, head tilted downward, tail drooped, and both wings hanging in front of, and well below, the perch.

Might there be sexual significance in those instances of both free and captive birds bringing the vent into close proximity to ants, either by direct application in that region or by holding the vent near the ground? Several of the American Robins, performing active anting, sometimes crouched, rotated or rubbed the body or breast upon the ground, or sat as if holding vent to ground (Nichols, 1943; Van Tyne, 1943; Brackbill, 1948). Ivor (letter, November 3, 1954) informs me that two of 12 Robins regularly crouched but that the others never took that position when anting. Certain of Poulsen's thrushes (*Turdus migratorius, T. musicus* and *T. philomelos*), while

applying ants, sometimes assumed passive anting posture. He writes that they "suddenly fluffed their feathers and spread both tail-feathers and wingfeathers, making 1–3 strokes with a single ant, which was then discarded. All the while they were sitting on the ground and allowing the ants to crawl on them without removing them. . . ." Lawrence (1945) cited a rather similar case for *migratorius*. Comparable photographs showing American Robins in partial crouch with this double-wing-spread appear in Ivor (1956) and Poulsen (1956). (Might these variations evident in *migratorius* be related to sex difference?)

Posture that would seem to expose the area of the vent to ants also has been described for some other species. Poulsen, as well as Brackbill, noted Common Grackles that repeatedly sat on the ground, with tails stretched out behind, while applying ants. A captive Rook flopped down on the anting area and raised its tail while the ventral body was flat on the ground; and a captive Carrion Crow pressed its tail against the earth while sprawling on the anting area (Goodwin, 1953a). Both of these last birds, though using passive anting posture, at times applied ants with the bill. Wackernagel's Carrion Crow applied ants but also lay flat on its belly with wings spread. While lying down, it several times struck here and there with its fanned tail. Once it sat, as if brooding, and rubbed the "anal area" on the ground. Sometimes it interruped anting to go to the turf and, with widely spread tail, drag its plumage through the grass. Simmons states that in the Magpie the ant sometimes quite definitely is "rubbed in the area of the vent" and he suspects this is true of many smaller birds whose quick motions are hard to observe in detail. Osmaston's (1936) birds, three or four species, using bugs (Rhynchota), rubbed them only "near the anus."

The foregoing descriptions relate to individuals that performed more or less active anting. As for those that stand, squat or lie and make few or no applications with the bill, the skin of the ventral body, including the vent, would seem especially vulnerable to ants and ant spray, particularly when the contour plumage is fluffed, as often seems the case during passive anting. And here we should bear in mind that ant spray may carry eight inches or more.

Captive European Jays showed "apparent attempts to bring the ventral areas in contact with ants by dragging them along on the ground" (Goodwin, 1951). These birds customarily brought forward or depressed the tail, spread *both* wings forward with convulsive, shuddering spasms, and constantly ran the bill down the wing quills without actually applying ants or even picking up ants. The insects swarmed up their legs and into their plumage. Goodwin's (1955b) sketches of some characteristic anting postures show this species in upright, almost penguin-like attitude, with undertail coverts (and vent?) apparently touching the ground, tail flat on the ground ANTING IN BIRDS

behind, and the posterior edges of the opened wings just brushing the ground. Like posture in this jay is shown here (Fig. 4) and in other photographs (Löhrl, 1956; Burton, 1955c) and descriptions (Goodwin, 1947; 1952a; Poulsen, 1956; Robien, *in* Stresemann, 1935b). Incidentally, Burton (*loc. cit.*) demonstrated its occurrence in response to substitute materials.

Scherping (in Stresemann, 1936) observed that a tame young Carrion Crow lying with spread wings on an ant heap never did apply the ants. Condry's tame young bird of this species behaved in much the same way but drooped the head in a "swooning" position until beak touched the ground, and sometimes it put ants on its back with the bill. Chisholm (1944) referred to a Magpie-Lark (*Grallina cyanoleuca*) that sprawled on the ant mound as if incapacitated. A young captive Hooded Crow lay with half-spread wings, flapped them as if bathing, but did not apply the ants (Coombs, 1947); and a tame Mistle Thrush pressed itself against the ground, wings spread, while ants crawled on its body (Moltoni, 1948).

Lühmann's Carrion Crows ruffled their plumage, lowered their breasts onto the ant nests, and made bathing motions. Lest this appear to have been mere dust-bathing, it should be added that Lühmann remarks that he was never able to see even an attempt at anting whenever few ants were present at the nest surface. Beebe's Northwestern Crows sprawled, almost as if dead, while ants crawled upon them, except that the head was held up to one side, exposing apteria at the back and shoulders.

As Löhrl and Condry state of the Carrion Crow, John A. Johnson's (letter, September 17, 1954) Common Crow permitted ants to cover it from neck to tail. When picked up from the ant bed before surfeit, the bird would return to the ants at once. It would stand until the insects began crawling up its legs, then would lie down on one side, with fluffed plumage and lifted wing, or again, on its breast with both wings slightly spread. Sometimes it "spread feathers at base of the tail" with its beak, apparently "to let ants reach the skin" but it was never seen to apply ants with the bill.

The above cases of passive anting are not altogether different from the behavior of certain mammals with ants. Bagg (1952) watched a gray squirrel (*Sciurus carolinensis*) roll and tumble on unidentified ants, and occasionally crawl on its belly across the nest. Swanson (1956) described a "timber squirrel" that rubbed its belly and head against a spot on the trunk of a maple tree where ants were feeding on the sap. And Chisholm (1948:163–175) mentioned the case of a domestic cat's (*Felis domesticus*) ecstatic contortions on a rubbish heap where ant-debris from a collector's can had been emptied. It may be significant that a fox and a squirrel evidently did not behave in any unusual way while eating termites (Stewart, 1888), and that anting with termites, which apparently do not liberate defense fluids, appears to be unknown in birds.

From cases reviewed here—and others could be cited—it seems clear that, as a result of either active or passive anting, a bird can receive ant substance upon the skin of the undertail region in proximity to the vent and probably on the vent. I believe further study may show a main focus for stimulation in many, if not all, anting birds to be the undertail region, probably the vent, hence the peculiar positions of the tail which sometimes cause tripping or falling.

In analyzing the literature pertaining to active anting, one is struck by the comparative rarity of instances involving application to dorsal body areas, or even dorsal surfaces of the quill feathers-these latter being favorite targets *ventrally*, according to most observers. Furthermore, such records usually indicate that the dorsal applications were few or that, in the main, the bird was anointing ventral areas of the wings, tail or body. Also, one notes that rump and upper tail coverts are mentioned more often than the other dorsal parts. One citation of application to the back in a young Dipper (Cinclus sp.) seems due to error in translation and should read belly (Bauch) instead (McAtee, 1938, citing Heinroth, 1911a). Anointment of the anterior body appears to be rare, except in grackles, and almost invariably is accompanied by treatment of wings and tail. It is noteworthy that three species of grackles (Icteridae), which are prone to anoint various parts of the body, wings and tail, usually have used one or more of eight substitute materials. Indeed, with these birds, the use of ants would seem to be the exception rather than the rule (see citations in Table 3). The observations of W. W. Worthington (letter, November 24, 1956) on two species of grackles in nature relate to use of limes and lemons on the wings, tail, breast, neck and scapulars, and are thus similar to the reports of several other persons. Poulsen (1956), ignoring passive and active anting as the two basic types of the behavior, recognized five types of anting, to one of which he assigned only his three Common Grackles (Quiscalus quiscula), on the basis of their applying ants to the breast, scapulars, rump and upper tail coverts, in addition to the wings.

It is significant also that generally those birds (seldom under 10 inches) which permit massive invasion of the plumage by ants seem not to apply ants with the bill, or seem to do so rather casually or sparingly. Since a good many of the commonly used spraying ants are capable of ejecting their spray with considerable force, may not these birds obtain the desired stimulation (of the ventral body skin) with no effort on their part other than that of standing, squatting or lying with spread wings and sometimes raised contour plumage? (Compare descriptions and the illustrations of Goodwin, 1952a, 1955b; Coombs, 1947; Condry, 1947; Lühmann, 1951; Wackernagle, 1951, with those of Brackbill, 1948; Groskin, 1950; Ivor, 1941, 1943, 1956.)

In a number of cases, birds behaving this way were known to settle down

Lovie M. Whitaker

among the ants only after ants had crawled up their legs (and stimulated body skin?). Wackernagel's bird went to spraying ants and stalked back and forth (increasing the quantity of ant spray?) before settling down among the insects or applying them with the bill. Robien's (*in* Stresemann, 1935b) European Jays trod upon ants as if to increase the spray; Condry's Carrion Crow, when ants crawled up its legs to the feathers, sat down among them like a brooding hen.

I have described the oriole's way of treating the distal portion of the tail in a follow-through of applications first made directly to undertail coverts and basal portions of rectrices. Could this extended dabbing, out along the ventral side of the tail, possibly be reflexive action, due to ant substances warming the skin of the undertail region? Might such stimulation cause some of the special movements of wings and tail reported in certain species?

The idea of special movements being reflex consequences of thermogenic agents on the skin may sound far-fetched unless we recall that some of these actions evidently occur *after* ants have been applied or ant spray, presumably, has reached the skin.

Goodwin (1947, 1952a, 1953a) clearly showed European Jays standing among spraying ant species and assuming their double-wing-spread posture only after ants had swarmed up their legs, in one case after they had reached the ventral body plumage. He and Poulsen both found that this species, the Green Magpie (Kitta chinensis), and the Red-billed Blue Magpie (K. erythrorhyncha) would advance both opened wings, accompanied by convulsive shudderings. Each of these species let ants swarm into the plumage; none actually applied ants, although they went through the motions of doing so. Poulsen's Blue Sugarbird (Dacnis cayana) took like posture. He (1956:274) wrote "This species picks up an ant [spraving species] 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 ant was eaten or discarded afterward. Pillai (1941) noticed Indian Mynahs spreading and quivering the tail during active anting in the midst of a colony of Oecophylla smaragdina, a spraying ant species. Tebbutt and Stone each mentioned shaking of wings or tail in anting birds, and other instances are cited elsewhere in this paper. Sick (1957) noticed that a free-living Blue-necked Tanager (Calospiza cyanicollis) sometimes cocked its tail upward during active anting. Some of these acts bear remarkable resemblance to certain movements of sexually-motivated birds, as discussed by Armstrong (1947), Hinde (1955; 1956), Moynihan (1955) and others.

Another parallel sometimes is seen between the postures of sun-bathing and those of anting, particularly passive anting. Beebe's (MS) Northwestern Crows sprawled on ant nests with their heads "generally held off to one side to expose the fold of naked skin between the feathers of the back and scapulars. . . The nearest similar behaviour I have observed is that caused by sudden exposure to sun when a bird has been in shade for some time." Condry (1947) and Goodwin (1953a) described much this same posture in anting Carrion Crows. The behavior of Burton's (1955a) Rook, already mentioned, when exposing itself to electric heat and to steam, may have been analogous to sun-bathing. Other sun-bathing attitudes suggestive of anting postures can be found in Hauser (1957), Rollin (1948), and Gibb (1947).

Hauser (op. cit.) showed that free birds, sunning themselves on a brown masonite feeding tray or on a leafy compost heap, were exposed to surface temperatures as high as 140° F. She said that heat alone did not seem to be the primary factor. Yet her "Compulsory Sun Position," as distinct from "Voluntary" sunning, deserves critical study in the light of birds' anting responses to thermogenic materials. Certain of her descriptions and sketches showing intense, involuntary sun-bathing posture seem very much like some of the attitudes described for anting, in situations where, apparently, the only heat involved was in the anting material itself. (Compare, for example, Hauser's sketch of sunning Mockingbird, *Mimus polyglottos*, with Goodwin's [1955b] sketch of anting Rook.)

Another point that may prove of considerable importance to better understanding of anting is that passive anting appears to be extremely rare, if it occurs at all, with non-spraying ants. Except for Galloway's (1948) brief statement that a Magpie-Lark which he saw picking up and squeezing *Iridomyrmex detectus* "did not mind the ants crawling about its feathers," all cases I have seen of *identified* ants invading a bird's plumage have concerned spraying species. Unfortunately, Galloway did not describe the Magpie-Lark's posture, or state whether it was applying ants or only feeding on them. Both Goodwin (1951) and Lühmann mentioned negative response in passively anting birds when few ants were present. This seems quite different from actively anting birds which, in a number of instances, have been known to respond to one or few ants; and it suggests that a considerable amount of spray may be required for passively anting birds to assume anting posture. It would be instructive to learn whether the passively anting Common Crow, for instance, would respond at all to non-spraying ants.

In considering the premise that anting birds, at least in some cases, are trying to get thermogenic materials on the ventral body skin, we should not neglect smoke as an anting substance. IJzendoorn, Chisholm (1948:163– 175), and others, have discussed smoke in connection with anting. It has been suggested that smoke may be satisfying for its warmth or the thermogenic effects of acids contained in it. Doubtless this is true also of many other substitute materials, such as beetles, earwigs, millipedes, wasps, prepared mustard, and some of the other vegetable materials. The use of hair tonic, previously mentioned, is of unusual interest, for Dr. Fluck wrote me that the lotion contained, in addition to bay rum and alcohol, tincture of cantharides. Cantharides are dried beetles (usually *Cantharis vesicatoria*, *C. vittata*, or *Mylabris cichorii*), which have the vesicant constituent cantharidin, as well as uric, formic and acetic acids. Of pungent, acrid taste and penetrating, aromatic odor, these insects are used in medicine as a counterirritant, blistering agent, diuretic and aphrodisiac (Youngken, 1948:920; Mansfield, 1937:463).

Some species, even individual birds, seem to perform with smoke exactly as they do with ants and certain substitutes. I have already mentioned how various burning or smoking materials were applied by a Rook and a European Jay. Burton's descriptions and the photographs of these two individuals follow closely Goodwin's descriptions and sketches of these same species when using ants (Burton, 1955*a*, 1955*b*, 1955*c*; Goodwin, 1952*a*, 1955*b*). Although it also used ants, Burton's Rook consistently gave strong, typical anting responses to smoke of any kind. A captive Blue Jay, a species with pronounced anting proclivities, applied burning cigarettes (Miller, 1952), and another such individual held them in the bill, apparently in order to get smoke under its wing (Anon., 1952).

A most unusual account of birds using smoke concerns the small flock of Red-browed Waxbills (Estrilda temporalis) at Kairi, on Atherton Tableland, North Queensland, which Givens (1945) observed on several days in June. The birds, as many as a dozen at once, would stand on a smoldering log, in the curling wisps of smoke coming up through cracks in the bark, and there perform anting movements "quite distinct from those commonly seen when birds bathe in dust or water". Each bird would stand upright, with tail as "support" and wings drooping a little forward and downward, and begin sweeping the head forward and down under the wings, meanwhile vigorously shuffling its wings and body feathers and "often toppling backward from the violence of its efforts." Givens, watching from a distance of about six feet, saw no insects on the log, nor could he find any afterward. But he does say that on one occasion "when a piece of bark was torn away from a nearby stump," revealing an ant nest, one of the birds "tried to ant itself there, but soon abandoned the attempt in favour of the smoke." Sometimes a bird, unable to find space in the smoke, performed a few feet away, much as a bird may water-bathe in vacuo.

Elsdon (1948) described Linnets (*Carduelis cannabina*), Meadow Pipits (*Anthus pratensis*) and Pied Wagtails (*Motacilla alba*) that for several days in August and September persistently flew into thick smoke from a huge oil-tank fire, at times flying as low as about 50 yards above the flames. Sometimes birds would alight exhausted near the observers, only to fly back into the smoke when they apparently had recovered. Jackdaws (*Corvus*)

monedula) repeatedly have hovered briefly in chimney smoke (Ridley, 1948), while Common Starlings and Rooks have perched in such smoke and ruffled their feathers (Prideaux, 1947; McMeeking, 1949). One of the Rooks performed "contortions" in the smoke.

These records of free birds frequenting smoke do not indicate that the smoke was flushing out insects and thus attracting the birds, as may be the case during grassland fires. Although some of the incidents occurred during winter in England, others of them occurred there in June, August and September, when birds may not have been trying to escape cold. Among winter records, when the insect factor would seem improbable, are some that mention preening and posturing in the smoke.

Excepting the Linnets, Meadow Pipits, Pied Wagtails, Jackdaws and possibly the Red-browed Waxbills, all birds mentioned thus far here in connection with smoke have been species known also to use ants or the more conventional substitutes. It is interesting to see that Poulsen (1956) found anting in the Tree Pipit (Anthus trivialis).

The other smoke-bathing records that I have seen relate to species not known to ant: Herring Gull, *Larus argentatus* (White, 1948; Stevens, 1948); Black-headed Gull, *L. ridibundus* (Stevens, 1948; Stafford, 1954); Little Owl, *Athene noctua* (Tubbs, 1953); Swift, *Apus apus* (Adler, 1954); Welcome Swallow, *Hirundo neoxena* (Barker, 1939); and House Martin, *Delichon urbica* (Pritchard, 1950).

I find no records of "smoke-bathing" as such in the Western Hemisphere; however, Dr. Arthur A. Allen tells me that he once had a tame Common Crow that liked to get into smoke from an incinerator, and there is the instance of Bluebirds (*Sialia sialis*) and Cedar Waxwings (*Bombycilla cedrorum*), which last species is known to ant, warming themselves on a chimneytop in sub-zero weather (Parker and Parker, 1950).

Chisholm (1948:163-175), reviewing the problems of anting, commented: "'Smoke-bathing' may in fact be complementary to water-bathing, sunbathing and dust-bathing, and all four may well be allied to 'anting' with acids."

SUMMARY

Intensive study of anting behavior in a captive Orchard Oriole (free of obvious ectoparasites) with worker ants of several species during a 31-month period showed the bird's basic anting pattern was similar to that described for most small species, but new or different in several aspects.

To summarize present knowledge and for purpose of comparison, an analysis was made of all available anting records, including some unpublished materials.

The compiled list of 148 species of anting birds includes 65 New World forms. Types of anting, theories concerning its significance, and the possible relationship of anting to dust-bathing and sun-bathing are reviewed. Two basic types of this behavior are recognized: *active* anting (anointing by use of the bill) and *passive* anting (anointing by allowing ants to invade the plumage).

Offered seven non-spraying ant forms, the Orchard Oriole exhibited consistent selectivity in choice of species for anting. Differences in odor, flavor and defensive mechanisms of acceptable and unacceptable ant species are described, the most important being that all acceptable ants (three species) were found to produce a burning sensation on the human tongue, whereas the four unacceptable ant forms did not. This effect cannot be ascribed to the non-caustic butyric acid believed to be produced by all ant species the oriole accepted. The thermogenic agent in these ants has not been determined.

It appears that all ant species used by birds for anting may have thermogenic properties. Most species used are producers of formic acid, and may be presumed to be similarly stimulating. Since many substitute materials used for anting are also of this nature, "heat" seems to be the common factor in most, if not all, anting situations.

A synopsis of the known and *identified* ants used by birds for anting indicates that birds in general are selective. With one exception (probably a conditioned response), birds seem to have used only species that either spray or exude repugnatorial fluids. The ability of spraying ants, at least *Formica* rufa and its allies, to eject a fine mist to a distance of 20 to 50 cm. is an important factor in anting that may not have been generally recognized.

The Orchard Oriole applied ants by dabbing, not stroking. At the same time it rapidly vibrated its head. Regularly the bird anointed ventral surfaces of wing tips and of the base of the tail, and also the undertail coverts. Sides and flanks were touched only indirectly as the bird reached its vibrating head around toward wing or tail. Occasionally feathers of the belly and tibiae were anointed. Undertail coverts and bases of the rectrices received the most attention. Following the performance of anting with non-spraying ants, the bird was found to have ant odor on all these areas but not on other plumage tracts. The bird apparently crushed the ants before applying them. Crushing was found to increase the odor and thermogenic effect to the human tongue.

Tripping and tumbling occurred regularly, resulting from interference of the tail, which was brought forward beneath the body during anting. Often the bird performed while clinging to the cage wall, at times anting in an upside-down position.

Sometimes the oriole gathered and held in the bill a large wad of ants before applying, discarding or eating it. Occasionally it selected and ate certain bits of ant-nest earth, possibly soil impregnated with ant exudations. Ordinary earth was not eaten. Positive anting response was high in this bird. Of 80 contact days, it performed on at least 67. Negative response due to surfeit was rare. The longest period of successive daily performance was 10 days. Anting sessions, often lasting 45 minutes, became shorter as ants were offered daily. Physical stress of high intensity anting caused noticeable fatigue.

Drowned, frozen, or heat-killed ants elicited pronounced anting reaction, except when the treatment caused loss of thermogenic property (i.e., through heat-kill or long-term freezing).

The oriole distinguished variations among living worker ants of the colony, applying some individuals repeatedly, others only once, and discarding some without use. Taste-testing showed marked thermogenic variation among worker ants of a colony. Apparently the bird used most assiduously those individuals having strong heating value. This property of the ant seemed less pronounced in winter than in summer, and may be a cause of the bird's somewhat milder anting response in winter. The bird was not interested in ants primarily as food.

Preening and bathing following anting were erratic and seemed caused as much by physical exertion and displaced plumage as by the possible effect of ant-ointment on the feathers.

These non-spraying ants caused no unusual blinking or spreading of nictitating membrane, frequently reported in birds using spraying ants.

Records of anting in birds obviously infested with ectoparasites appear to be extremely rare. Endoparasites as a factor in anting should be investigated. No report of an autopsy of an anting bird could be found, or even of microscopic examination for smaller ectoparasites. Literature examined failed to indicate that captivity either causes or suppresses anting or modifies significantly the specific anting patterns.

The cause of anting in the Orchard Oriole was not determined. The bird's preferential treatment of the undertail region, and possibly the vent itself at times, was indicated by direct observation, by extreme displacement of undertail coverts, and by the fact that ant odor was strongest here. Close study showed this region received additional treatment when wing tips were anointed, due to juxtaposition of the wing tip with the tail.

Although there was no evidence of gross ectoparasitism in the oriole, it is possible that ant substances relieved itching caused by minute ectoparasites or cysts of endoparasites, certain species of which are known to occur in skin of the undertail region of birds. Also, the bird appeared to derive sensual pleasure, possibly including sexual stimulation, from the thermogenic effect of the ants. The concept of sexual stimulation might throw light on several peculiar features sometimes seen in anting behavior, such as pressing and rubbing of vent upon the anting ground, drooping-wings posture following anting, convulsive shuddering and quivering in conjunction Lovie M. Whitaker

with a double-wing-spread stance, quivering or shaking of wings and tail, individual differences in the amount and in the occurrence of anting among captives of a species, and the apparent irregularity with which birds seem to ant in nature.

Several facts, derived from study of the literature and considerable reading in the field of myrmecology, may bear upon the problem. First, it is physically possible for ant substances to touch a bird's ventral posterior skin (including the vent) during either active or passive anting, due to ability of a bird to reach this area with its bill (shown in many anting descriptions and commonly seen in preening), and to the spraying force of ants. Secondly, passive anting with non-spraying ant species appears to be almost unknown; and, unlike active anting, it often entails raising of the contour plumage. Thirdly, while anointment of plumage and skin must become general when a bird permits spraying ants to invade its feathers in numbers, species (excepting grackles) that practice active anting apparently seldom or never apply ants to the anterior part of the body, the dorsal body or even to dorsal surfaces of quill feathers.

Certain apparently aberrant anting motions, seen in the Orchard Oriole or reported in literature (incipient or desultory applications, anointment of unusual feather tracts), may possibly be due to inadequate amount of stimulant in the individual ant or in the substitute material used. The oriole's reactions to frozen and to heat-killed ants (stimulant reduced or destroyed) suggest correlation between the amount or degree of the thermogenic agent and the plumage area treated. This topic needs further investigation.

In recognizing "heat" as the common anting factor, smoke must be given consideration as an anting substance. Smoke-bathing appears virtually unknown in the Western Hemisphere. Instances of species, even individuals, performing alike with ants, smoke, and burning or heated materials, all seem cases in point.

This study demonstrates the importance of entomology to any solution of the anting problem. In common with others, it contributes little toward understanding why certain species of birds will ant while others apparently do not, but it does show that new species are continually being added to the list of anting birds. The fact that a species has not been reported does not necessarily mean that it does not ant. Likewise, it is risky to conclude that the anting response is absent in a species merely because individuals have refused to ant.

Many questons raised here cannot be answered short of controlled experiments on a large scale. Perhaps this résumé will provide an impetus for thoroughgoing experimentation, particularly with Common Crows (passive anting) and Blue Jays or Common Starlings (active anting), inasmuch as anting incidence seems to be unusually high among these species.

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262