CHAPTER 4

AVIAN CHEMICAL DEFENSE

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1. INTRODUCTION

Many vertebrates use noxious or deterrent chemicals as defense against predators, parasites, and/or microbes. Putatively adaptive chemical defenses have been described for fish, salamanders, frogs, toads, snakes, lizards, and even mammals. For some of these groups, e.g., frogs and toads, chemical defense may be the primary means of protection from predation. In contrast, no birds are listed in recent indices of chemically-defended animals (see Species Index, *Toxicon* Vol. 1–27, 1990), and birds have generally been thought not to use chemical defense.

Recently, however, three bird species in the genus *Pitohui* were found to contain the potent alkaloid neurotoxin homobatrachotoxin (Dumbacher *et al.*, 1992). The concentrations of homobatrachotoxin in the Hooded Pitohui (scientific names are given in Tables I and II except for species only mentioned in the text) can be relatively high; simply holding a bird from some populations can cause a human to sneeze and have watery eyes and irritated lips (Salvadori, 1881; Kocher-Schmid, 1991, 1993; Dumbacher, 1994). Furthermore, the relative concentra-

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tions of homobatrachotoxin in various tissues of pitohuis also suggest that the toxin could serve as a powerful deterrent to predators or parasites. Toxin concentrations are highest in the feathers and skin, intermediate in muscle, and lowest in the internal organs (Dumbacher *et al.*, 1992). If homobatrachotoxin deters predators (Diamond, 1992; Dumbacher *et al.*, 1992, 1993) or parasites (Mouritsen and Madsen, 1994; Poulsen, 1994) that would otherwise reduce the fitness of individuals, then it is plausible that the manufacture or use of this chemical by pitohuis represents an evolved adaptive response by the birds, and homobatrachotoxin serves as a chemical defense.

The identification of homobatrachotoxin in pitohuis led to the initial interpretation that these were the world's only poisonous birds. This is not, in fact, the case. The Eurasian Quail (Lewis *et al.*, 1987), Spur-winged Goose (Eisner *et al.*, 1990), and Red Warbler (Escalante and Daly, 1994), for example, also contain toxins that may serve as chemical defenses. Additionally, many other species (see Tables I and II) contain toxic or unpalatable chemicals that may help defend them, either directly or indirectly, against predators or parasites. Furthermore, chemical defenses used by birds may also take the form of behavioral application of deterrent chemicals. In many species, individuals apply ants, plant products, or chemical compounds directly to their feathers, their skin, or to their nest, presumably to reduce parasite or microbial infestations (e.g., Clark and Mason, 1985, 1988; Ehrlich *et al.*, 1986; Clayton and Vernon, 1993).

It is not entirely clear why the topic of avian chemical defense has received so little attention. Detailed studies have shown how birds use chemicals (Swennen, 1968, 1974; Clark and Mason, 1985, 1988; Clayton and Vernon, 1993), and the defensive properties of some avian chemicals have been documented (Jacob, 1978; Clark and Mason, 1985, 1988). Additionally, the relative palatability of birds to potential predators has been extensively studied (Cott, 1946; Cott and Benson, 1970; Goodman and Hobbs, 1990). One possibility may be that the number of cases in which birds are poisonous to predators is relatively small, and that, prior to the studies of Eisner *et al.* (1990) and Dumbacher *et al.* (1992), in no case had the chemical involved in avian toxicity been identified, its structure described, and its toxic effects on other vertebrates demonstrated through laboratory bioassays. Nevertheless, chemical defense in birds may be much more common than previously thought (Cott, 1946), and several authors have argued that important work in this area has been overlooked (Pough, 1992; Wrangham, 1992; Götmark, 1994a).

In this chapter we review available evidence for chemical defense in birds and examine that evidence from both an ecological and evolutionary perspective. Because our present understanding of the ecology and evolution of chemical defense is generally based upon studies of taxa other than birds, it is our hope that this review will provide the basis for inclusion of birds in future discussions of this topic. In other taxa, chemical defense is correlated with aposematic coloration (Cott, 1940; Guilford, 1990), mimicry (Bates, 1862; Müller, 1879; Brower, 1984) and gregariousness (Fisher, 1927; Sillén-Tullberg, 1988, 1990). Authors have suggested that similar correlations may exist in birds (Cott, 1946; Barnard, 1979; Diamond, 1992), and we review the available evidence for these hypotheses.

2. DEFINITIONS AND OVERVIEW

To avoid confusion it is first important to explicitly define chemical defense. There are several published definitions. For example, Brower (1984) offered the following:

> Chemical defense exists in a species when individual prey organisms contain one or more chemical substances which facilitate proximal and or distal rejection by predators or parasites; rejection can occur after a predator partially to completely ingests one or more prey individuals, or after the predator (or parasite) simply smells or tastes the prey.

In reference to chemical defenses in plants, Rausher (1992) suggested a more restrictive definition. He defined a defensive trait as "any resistance trait that has evolved or is maintained in a population because of selection exerted by . . . natural enemies."

We consider both of these definitions inadequate for birds. Brower's does not allow for application of deterrent chemicals to the nest environment. Rausher's definition does not separate the chemical interaction between species from the evolution of those interactions. Furthermore, the evolutionary origin or maintenance of defense, in most cases, is difficult or impossible to document, making Rausher's definition difficult to apply operationally. We propose the following definition: "Chemical defense occurs when an individual contains or uses behaviorally one or more chemical substances that deter predators and/or parasites." Our definition includes all known types of chemical defenses in birds, encompasses common usage of the term, is sufficiently general to permit extension to other taxa, and focuses on the chemical interaction between species, which we feel is the crux of chemical defense. It also implies methods for testing or identifying chemical defense. To identify chemical defense, it is necessary to show that 1) individuals contain or use a chemical(s) that elicits rejection or avoidance by predators, parasites, and/or microbes, and that 2) in the absence of the chemical(s), the individuals would experience a decrease in fitness attributable to the target organism (predator, etc.).

Although we will argue that many cases of chemical defense in birds represent adaptive evolution, the question of evolution is separate from, but obviously related to, the identification of chemical defense. Chemical defenses can evolve through mechanisms other than natural selection imposed by predators or parasites (see section 6). Furthermore, although the occurrence of chemical defense implies that predators and other target organisms have the sensory capabilities to detect the deterrent, the identification of a substance as a chemical defense does not necessarily imply a particular sensory mechanism of detection. Certain types of chemical defense (e.g., unpalatability associated with aposematic coloration) also imply that predators, etc., have the ability to learn from their aversive experiences with chemically-defended individuals, but this is not true of all types of chemical defense. Avoidance or rejection of potential prey or hosts can occur through learned, conditioned responses or through unlearned responses to pain or irritation.

There are two categories of avian defensive chemicals: toxic and unpalatable. These categories roughly correspond to the designation by Brower (1984) of Class I compounds (toxic) and Class II compounds (unpalatable). Toxic compounds are those that can cause physical or physiological damage or malfunction to a target organism when encountered in a biologically relevant fashion. Unpalatable compounds are innocuous substances that cause a harmless, but aversive, reaction to one or more receptor systems in a target individual. Some defensive chemicals fit neatly into one classification; for example, methyl anthranilate is not toxic but is so unpalatable to birds that it is a powerful repellent (Kare and Pick, 1960; Clark and Shah, 1991; Clark *et al.*, 1991). Nevertheless, the distinction between the categories is sometimes vague. Some chemicals, such as strychnine, are both highly toxic and unpalatable to many vertebrates. Furthermore, some toxic chemicals may occur at concentrations too low to be poisonous but may still act as unpalatable chemicals.

3. CHEMICAL DEFENSES IN BIRDS

Avian chemical defenses can be categorized according to the type of defensive chemical involved in the defense. We label these categories

chemical defense through toxicity, and chemical defense through unpalatability. Chemical defense through toxicity includes examples in which the individual bird becomes toxic or in which birds use toxic compounds in a behavioral way to achieve defense.

With respect to the dynamics and evolution of each of the two broad categories of defense, the most important issues are 1) what deterrent chemical(s) are involved; 2) how a species obtains, sequesters, or synthesizes the deterrent chemical(s); 3) how the defended species advertises its defense; 4) how target animals (predators, parasites, etc.) detect the chemical(s); 5) how the chemical(s) affects target organisms; and 6) which target organisms are repelled. For most bird species exhibiting chemical defenses, these questions remain unanswered or are issues of speculation. In our review we discuss these issues when available data permit.

3.1. Chemical Defense through Toxicity

3.1.1. Bird Species that Are Toxic

Thirteen bird species are known or believed to be toxic. The nature of the documentary evidence for these cases, however, varies and we separate the examples according to the strength of that evidence (Table I).

Toxic chemicals have been identified for five species in two genera. Species in the New Guinea genus *Pitohui* are toxic. The Hooded, Variable, Rusty, and Black Pitohuis carry the alkaloid neurotoxin homobatrachotoxin (Dumbacher *et al.*, 1992; Dumbacher and Daly, unpublished data). Prior to its discovery in pitohuis, homobatrachotoxin was known only from poison-dart frogs (*Phyllobates*). Homobatrachotoxin is a member of a family of steroidal alkaloid toxins, collectively called batrachotoxins, which are among the most toxic natural compounds known in vertebrates (Albuquerque *et al.*, 1971). Batrachotoxins bind sodium channels in a wide variety of tissues and depolarize electrogenic membranes in nearly every vertebrate and invertebrate species tested (Daly and Spande, 1986; Dwivedy, 1988; Soderlund *et al.*, 1989).

In laboratory assays, subcutaneous injection of ethanol extracts from macerated skin of the Hooded Pitohui caused convulsions and death in laboratory mice (Dumbacher *et al.*, 1992). Of the four species of pitohui, the Hooded contained the greatest amount of toxin (about 18–24 μg homobatrachotoxin total in a 65 g individual), the Variable Pitohuis contained 7–12 μg (in a 85–95 g individual), and the Rusty Pitohuis contained about 1–3 μg (in a 100 g individual; Dumbacher *et al.*, 1992). Feathers from two individual Black Pitohuis contained con-

TABLE I
Bird Species that Are Toxic or Use Chemicals Maleficently

Bird species[a]	Chemicals and origin	Nature of effect and comments	Reference
Category 1: Species that are toxic and from which the toxic chemical has been identified			
Spur-winged Goose *Plectropterus gambensis*	Cantharidin toxin from ingested beetles	Topical skin vesicant, systemic toxin	Carrel and Eisner, 1974; Eisner *et al.*, 1990
Pitohuis (Hooded, Rusty, Variable, Black) *Pitohui dichrous, P. ferrugineus, P. kirhocephalus* and *P. nigrescens*, respectively	Homobatrachotoxin, origin unknown	Binds Na+ channels, disrupts nerve and muscle function	Salvadori, 1881; Majnep & Bulmer, 1977; Kocher-Schmid, 1991; Dumbacher *et al.*, 1992; Dumbacher and Daly, unpublished data
Category 2: Species with unknown toxic chemicals whose deterrent effects have been studied			
Eurasian Quail *Coturnix coturnix coturnix*	Unknown, presumably sequestered from diet	"Coturnism"—nausea, muscle pain, rarely death	Sergent, 1948; Kennedy and Grivetti, 1980; Lewis *et al.*, 1987
Red Warbler *Ergaticus ruber*	Unidentified alkaloids	Currently under investigation	Escalante and Daly, 1994
Category 3: Species whose reported toxicity requires confirmation			
Ruffed Grouse *Bonasa umbellus*	Andromedotoxin, from feeding on mountain laurel in winter months	Toxic, has caused human deaths after ingestion	Wilson and Bonaparte, 1831; Bicknell, 1960
Carolina Parakeet *Conuropsis carolinensis*	Unknown, possibly sequestered from cocklebur seeds	Accumulates in internal organs, has caused death in domestic cats (*Felis domesticus*) and dogs (*Canis familiaris*)	Wilson and Bonaparte, 1831; Audubon, 1929
African Olive-Pigeon *Columba arquatrix*	Unknown, putatively from *Podocarpus* berries	Affects kidneys, poisonous if eaten constantly	Jackson, 1926
Mauritius Pink Pigeon *Columba mayeri*	Unknown, sequestered from diet	Irritates and numbs mouth and throats in humans	Temple, 1987, 1994
Common Bronzewing *Phaps chalcoptera*	Unknown, potentially flouroacetate, from the plants *Gastrolobium* spp. and *Oxylobium* spp.	Has caused convulsion and death in domestic dogs that ingest pigeon bones and viscera	Gardner and Bennetts, 1956; Austin and Singer, 1973; Main, 1981
Brush Bronzewing *Phaps elegans*	Unknown, potentially flouroacetate, from the plants *Gastrolobium* spp. and *Oxylobium* spp.	Has caused convulsions and death in domestic dogs that ingest pigeon bones and viscera	Gardner and Bennetts, 1956; Austin and Singer, 1973; Main, 1981
Category 4: Species that maleficently use chemicals			
Northern Fulmar *Fulmarus glacialis*	Stomach oils, composed of partly digested fish oils	Oil is spit at enemies, soils feathers and hair	Swennen, 1974; Warham *et al.*, 1976

[a] Nomenclature and taxonomy of birds follow that of Sibley and Monroe (1990).

centrations of toxin roughly equivalent to those in the Rusty Pitohui (Dumbacher and Daly, unpublished data). For individual pitohuis of each species, Dumbacher *et al.* (1992) estimated that about 85% of the total toxin was in the skin, 11% in the feathers, and the remainder in muscle tissue and internal organs.

The Hooded Pitohui effectively deters human predators and is avoided as a food source by many native peoples of New Guinea. The meat tastes bitter and causes allergy-like reactions; humans may become nauseated from simply smelling the bird (Majnep and Bulmer, 1977; Kocher-Schmid, 1991, 1993). In addition to humans, natural predators or parasites are believed to be detered by homobatrachotoxin in pitohuis (Dumbacher, unpublished data; Mouritsen and Madsen, 1994).

As is true for poison-dart frogs, the source of the toxin in pitohuis is not known. Homobatrachotoxin has not been identified in any plants or insects. In the Hooded Pitohui, toxin concentrations vary geographically, which may suggest a dietary source of toxin whose availability also varies geographically. In some areas the toxin can be detected only through laboratory analysis of tissue, but in others simply holding a bird close to one's face can cause nasal irritation and watery eyes. If natural predators have sensory capabilities similar to those of humans, then it is possible that predators could detect the toxin before killing or injuring an individual pitohui.

The toxin cantharidin has been identified in Spur-winged Geese from the Niger River in Africa (Eisner *et al.*, 1990). Cantharidin is produced by beetles (of the family Meloidae) that are eaten by the geese. The toxin was identified by diagnostic toxic effects of cantharidin in human males who had eaten goose meat. No reported studies have quantified the amount of cantharidin present in individual geese or tested whether the toxin repels enemies. Frogs also sequester cantharidin from beetles, and 200–400 g of affected frogs legs can contain enough toxin to be fatal to humans (Eisner *et al.*, 1990). In laboratory studies, systemic cantharidin sequestered by frogs does not protect the frogs from leech ectoparasites or snake predators (Eisner *et al.*, 1990).

The bird longest known to be toxic is the Eurasian Quail. The symptoms of quail poisoning, or "coturnism," vary across individual human victims but include muscle pain, nausea and vomiting, fever and chills, general weakness, and possible temporary paralysis (Lewis *et al.*, 1987). Coturnism may ultimately cause respiratory difficulty and occasionally death. Other animals, such as domestic dogs (*Canis familiaris*), have also been known to suffer coturnism (Sergent, 1941).

Coturnism occurs only when quail from certain regions are eaten and at certain times of the year. The species is toxic during its northward migration, in northern Algeria and southern France, and during its southward migration, on the islands of Lesbos and Chios and in the region between the Black and Caspian seas (Lewis *et al.*, 1987). During migration, Eurasian Quail eat poisonous plants such as hemlock (*Conium maculatum*), hellebore (*Hyoscyamus niger*), and black morelle (*Solanum nigrum*), and they may accumulate the toxins from these foods (Sergent, 1941, 1948; Kennedy and Grivetti, 1980). Other potential sources of toxins include the mint *Stachys annua* and other members of Lamiaceae, as well as water dropwort (*Oenanthe crocata;* Sergent, 1948; Lewis *et al.*, 1987). The chemical responsible for coturnism has not yet been positively identified.

Even during migration, only a small proportion of Eurasian Quail cause coturnism when eaten. Furthermore, people poisoned by quail do not stop hunting or eating them, even after multiple serious intoxications (Lewis *et al.*, 1987; Grivetti and Rucker, 1994). This evidence suggests that the chemicals that cause coturnism do not deter human predators. It is not known whether non-human predators avoid toxic quail.

The Red Warbler in Mexico is also toxic. Indigenous folklore claims the bird is inedible, and the bird's feathers carry bioactive chemicals that extract into alkaloid fractions (Escalante and Daly, 1994). In Table I we list additional bird species that reportedly contain toxins.

3.1.2. Topical Application

Many species of birds apply arthropods topically to their feathers and skin, a behavior known as "anting" (Simmons, 1966; Ehrlich *et al.*, 1986). Anting may be a form of "self-medication" (Clayton and Wolfe, 1993) and may deter parasites. Anting birds expose themselves to, and wipe themselves with, ants, millipedes, and other arthropods, rubbing them or enticing them into their feathers and sometimes eating them. Birds behave similarly when applying substances such as lime fragments, plant vegetation, or vinegar to their feathers (Clayton and Vernon, 1993). Because these substances contain arthropod repellents, authors have speculated that birds ant to reduce parasites (Ali, 1936; Simmons, 1966; Ehrlich *et al.*, 1986; Clayton and Vernon, 1993). Recently, however, tests of this hypothesis failed to show any difference in parasite loads between anting birds and control birds (Judson and Bennet, 1992).

3.1.3. Chemical Modification of the Nest Environment

Many bird species include fresh vegetation in the construction of their nests (Collias and Collias, 1984), and such vegetation may contain chemicals capable of acting as fumigants, repellents, and toxicants (Meyers, 1922; Johnston and Hardy, 1962; Clark and Mason, 1985). In a review of nesting habits of North American passerines, Clark and Mason (1985) found that species nesting in enclosed spaces, such as cavities or crevices, were significantly more likely to incorporate fresh vegetation into their nests than species building open nests. The function of preferential selection of green vegetation for nests has been studied most extensively in the European Starling (Clark and Mason, 1985, 1987, 1988, 1991). Clark and Mason found that in southeastern Pennsylvania, starlings line their nests with green sprigs of agrimony (*Agrimonia paraflora*), wild carrot (*Daucus carota*), fleabane (*Erigeron philadelphicus*), rough goldenrod (*Solidago rugosa*), red dead nettle (*Lamium purpureum*), and yarrow (*Achillea millefolium*). These plants have been shown in laboratory experiments to inhibit cultures of pathogenic bacteria and fungi. In field experiments, they inhibited population growth of the fowl mite (*Ornithonsyssus sylviarum*) and of a hematophagous louse (*Menacanthus*). The starlings appear to discriminate among nest materials in favor of those with potentially anti-parasite volatile chemicals.

Other birds also place plants containing bioactive substances in nests, presumably to reduce parasites. In India, House Sparrows (*Passer domesticus*) incorporate fresh leaves of the margosa tree (*Azadirachta indica*) in their nests throughout the breeding season (Sengupta, 1981). Margosa leaves contain β-sitosterol, which repels and prevents oviposition of arthropods (Ambasta, 1980). White-breasted Nuthatches (*Sitta carolinensis*) and Rock Nuthatches (*Sitta neumayer*) brush their nests with fresh plant materials and insects (including *Meloe* beetles, which exude vesicating oils), presumably as a chemical defense against parasites (Adamyan, 1965; Kilham, 1968, 1971).

3.1.4. The Maleficent Use of Chemicals

Maleficent use of chemicals occurs when birds use compounds in ways that damage, injure, or otherwise harm predators. These chemicals need not be toxic in a strict sense, but we classify them with toxic chemicals due to their capacity to inflict serious injury or harm to a target predator or prey. However, we acknowledge qualitative differences between defense due to toxic compounds and those due to maleficent use of non-toxic compounds.

When threatened, the Northern Fulmar ejects or propels musky stomach oils at intruders or competitors. Studies of captive fulmars show that they spit the oils at other birds with little provocation (Swennen, 1974). When the victims try to wash away the oils their feathers become waterlogged, they become unable to fly or swim, and they usually drown or die of hypothermia (Swennen, 1974). The Northern Fulmar is also called the "giant stinker" and is considered inedible owing to its strong musky scent (Cott, 1946). Although all procellariiforms have stomach oils, only species in the genera *Macronectes*, *Thalassoica*, *Daption*, *Fulmarus*, and *Pagodroma* spit the oils as a defensive behavior. It seems notable that all species in these genera nest on (but not under) the ground. The primary function of spitting stomach oils at potential predators is believed to be protection of the birds' nests (Warham *et al.*, 1976).

Stomach oils do, however, have other functions besides defense. The oils are derived from digested fish and contain vitamin A, vitamin D, and energy-rich lipids (Clarke and Prince, 1976; Warham *et al.*, 1976; Jacob, 1978), and adults feed stomach oils to nestlings.

3.2. Chemical Defense through Unpalatability

Studies have shown that palatable prey are eaten even when a predator is replete, while unpalatable prey are taken only when a predator is hungry (Marshall, 1902; Swynnerton, 1919; Brower and Brower, 1964). Predators appear to rank prey along a "palatability spectrum" (Turner, 1984) and, when partially fed or when given a choice, avoid prey of lower palatability (Swynnerton, 1916b; Cott, 1946, 1951; Brower and Brower, 1964). As unpalatable prey have a lower probability of being preyed upon, they are defended by chemicals to the extent that their unpalatability is caused by chemicals. We include malodorous species in this section because a malodorous condition can elicit an aversive response similar to unpalatability, but one that is mediated through olfactory systems.

The majority of data on unpalatability in birds comes from the experimental work of H. B. Cott (Cott, 1945a, 1945b, 1946, 1948, 1949, 1951, 1952, 1953, 1954; Cott and Benson, 1970). In Cott's experiments, he offered flesh of different bird species to humans, natural predators, and scavengers and assessed the relative "edibility" of each species of bird by scoring the consumers' preferences.

In Table II we list reported cases of unpalatability and/or a malodorous condition in birds. Species listed merely as unpalatable are those that authors described as tasting "unpalatable," "horrible," etc.

TABLE II
Bird Species that Are Unpalatable and/or Malodorous

Bird species[a]	Species for which reaction has been documented	Comments	Reference
Category 1: Unpalatable and malodorous species for which there is experimental demonstration of aversion			
Northern Shoveler *Anas clypeata*	Ferrets (*Putorius furo*), rats (*Ratus norvegicus*), humans	Unpalatable, malodorous, sprays noxious feces on nest	Dixon, 1893; Blanford, 1898; Baker, 1908; Cott, 1946; Swennen, 1968
Common Eider *Somateria mollissima*	Ferrets, rats, humans	Unpalatable, males more unpalatable; sprays noxious feces on nest	Cott, 1946 Swennen, 1968
Greater Honeyguide *Indicator indicator*	Humans	Unpalatable	Cott and Benson, 1970
Eurasian Hoopoe *Upupa epops*	Hornets, domestic cats, humans	Malodorous	Wood, 1862; Smith, 1868; Cott, 1946; Vaurie, 1973
Pied Kingfisher *Ceryle rudis*	Hornets, domestic cats, humans	Unpalatable	Cott, 1946; Cott and Benson, 1970
Black Cuckoo *Cuculus clamosus*	Humans	Unpalatable, bitter	Cott and Benson, 1970
Red-backed Shrike *Lanius collurio*	Hornets	Unpalatable	Cott, 1946
Lesser Grey Shrike *Lanius minor*	Hornets	Unpalatable	Cott, 1946
Masked Shrike *Lanius nubicus*	Hornets	Unpalatable	Cott, 1946
Eurasian Golden-Oriole *Oriolus oriolus*	Hornets	Unpalatable	Cott, 1946
White-tailed Wheatear *Oenanthe leucopyga*	Hornets, domestic cats	Unpalatable	Cott, 1946
Hooded Wheater *Oenanthe monacha*	Hornets, domestic cats	Unpalatable	Cott, 1946
Mourning Wheatear *Oenanthe lugens*	Hornets, domestic cats	Unpalatable	Cott, 1946
Category 2: Species reported to be unpalatable or malodorous			
Dusky Scrubfowl *Megapodius freycinet*	Humans	Malodorous, nauseating rotting smell upon death	Diamond, 1994
Grey-winged Francolin *Francolinus africanus*	Humans	Unpalatable after eating certain beetles	Blanford, 1870; Cott, 1946
Blood Pheasant *Ithaginis cruentus*	Humans	Unpalatable	Cott, 1946
Satyr Tragopan *Tragopan satyra*	Humans	Unpalatable, bitter	Cott, 1946
Kalij Pheasant *Lophura leucomelanos*	Humans	Unpalatable after eating forest yams	Baker, 1921
Western Capercaillie *Tetrao urogallus*	Humans	Unpalatable, has resinous turpentine flavor after feeding on pine needles	Lloyd, 1867; Morris, 1870; Dixon, 1893
Kelp Goose *Chloephaga hybrida*	Humans	Eggs and flesh unpalatable in Falkland Island races	Murphy, 1936
Common Shelduck *Tadorna tadorna*	Humans	Unpalatable	Yarrell, 1843; Morris, 1897; Cott, 1946
Falkland Steamerduck *Tachyeres brachypterus*	Humans	Unpalatable, malodorous	Cott, 1946
Black Scoter *Melanitta nigra*	Humans	Unpalatable, fishy, oily	Dixon, 1893; Simon, 1944; but see Yarrell, 1843; Morris, 1897
Surf Scoter *Melanitta perspicillata*	Humans	Unpalatable	Dixon, 1893; Simon, 1944
White-winged Scoter *Melanitta fusca*	Humans	Unpalatable	Simon, 1944

(continued)

TABLE II (*Continued*)

Bird species[a]	Species for which reaction has been documented	Comments	Reference
Smew *Mergellus albellus*	Humans	Unpalatable, fishy	Dixon, 1893; Baker, 1908
Common Merganser *Mergus merganser*	Humans	Unpalatable, fishy, oily	Dixon, 1893; Baker, 1908; Cott, 1946
Red-headed Woodpecker *Melanerpes erythrocephalus*	Falcons (*Falco* sp.)	Unpalatable	Temple, 1994
Great Spotted Woodpecker *Dendrocopos major*	Humans	Malodorous	Naumann, 1905; Cott, 1946
Northern Flicker *Colaptes auratus*	Falcons	Unpalatable	Temple, 1994
Eurasian Green Woodpecker *Picus viridis*	Humans	Malodorous	Naumann, 1905; Cott, 1946
Puffbirds Family Bucconidae	Humans	Malodorous, feces putative source of malodorousness	J. O'Neill, D. Willard, and D. Stoltz, personal communication
Silvery-cheeked Hornbill *Ceratogymna brevis* (presumably *Bycanistes cristatus* of Cott)	Domestic cats, humans	Unpalatable, bitter, acrid, nestlings malodorous	Swynnerton, 1916b; Cott, 1946
Southern Ground-Hornbill *Bucorvus cafer*	Humans	Unpalatable	Marshall, 1902; Cott, 1946
Green Woodhoopoe *Phoeniculus purpureus*	Humans	Unpalatable, malodorous uropygial gland secretion	Marshall, 1902; Jackson, 1938; Cott, 1946
Violet Woodhoopoe *Phoeniculus damarensis*	Humans	Unpalatable, malodorous uropygial gland secretion	Marshall, 1902; Cott, 1946
White-headed Woodhoopoe *Phoeniculus bollei*	Humans	Malodorous uropygial gland secretion	Jackson, 1938; Cott, 1946
Common Scimitar-bill *Rhinopomastus cyanomelas*	Humans	Malodorous uropygial gland secretion	Marshall, 1902; Cott, 1946
African Malachite Kingfisher *Alcedo cristata cristata*	Humans	Unpalatable	Cott, 1946
African Pygmy-Kingfisher *Ispidina picta*	Humans	Unpalatable	Cott, 1946
Brown-hooded Kingfisher *Halcyon albiventris*	Humans	Unpalatable	Cott, 1946
Striped Kingfisher *Halcyon chelicuti*	Humans	Unpalatable	Cott, 1946
Red-chested Cuckoo *Cuculus solitarius*	Humans	Unpalatable	Cott, 1946
Klaas's Cuckoo *Chrysococcyx klaas*	Humans	Unpalatable	Cott, 1946
African Emerald Cuckoo *Chrysococcyx cupreus*	Humans	Unpalatable	Cott, 1946
Greater Black Coucal *Centropus menbeki*	Humans	Malodorous, rotten smell upon death	Diamond, 1994
Hoatzin *Opisthocomus hoazin*	Humans, natural predators	Malodorous, from digestion	Kirke, 1898; Chubb, 1916; Cott, 1946
Smooth-billed Ani *Crotophaga ani*	Humans	Unpalatable, malodorous	Chubb, 1916; Davis, 1940; Cott, 1946; Brown, 1974
Guira Cuckoo *Guira guira*	Humans	Malodorous	Davis, 1940
Alpine Swift *Tachymarptis melba*	Humans	Unpalatable, bitter, almost astringent	Cott, 1946
Fischer's Turaco *Tauraco fischeri*	Humans	Unpalatable, bitter	Cott, 1946
Ross's Turaco *Musophaga rossae*	Humans	Unpalatable, causes vomiting	Cott, 1946
Common Wood Pigeon *Columba palumbus*	Humans	Unpalatable after feeding on turnip greens	Bolam, 1913

(*continued*)

TABLE II (*Continued*)

Bird species[a]	Species for which reaction has been documented	Comments	Reference
African Olive-Pigeon *Columba arquatrix*	Humans	Unpalatable, bitter after eating *Podocarpus* berries	Jackson, 1926
Pale-vented Pigeon *Columba cayennensis*	Humans	Unpalatable, varies according diet	Chubb, 1916; Cott, 1946
European Turtle-Dove *Streptopelia turtur*	Humans	Unpalatable, bitter after feeding on wild olives	Cott, 1946
Bruce's Green-Pigeon *Treron waalia*	Humans	Unpalatable, bitter after feeding on wild olives	Cott, 1946
New Zealand Pigeon *Hemiphaga novaeseelandiae*	Humans	Unpalatable, bitter or turpentine flavor	Buller, 1882
Sarus Crane *Grus antigone*	Humans	Unpalatable	Elyot, 1541; Cott, 1946
Long-billed Curlew *Numenius americanus*	Humans	Unpalatable after feeding in salt marshes or coastal areas, palatable inland	Wilson and Bonaparte, 1831; Cott, 1946
Greater Yellowlegs *Tringa melanoleuca*	Humans	Unpalatable after feeding on horseshoe crabs	Herbert, 1853; Cott, 1945a
Snowy Sheathbill *Chionis alba*	Humans	Unpalatable	Wood, 1862; but see Cott, 1946
Eurasian Oystercatcher *Haematopus ostralegus*	Humans	Unpalatable	Naumann, 1905
Red-wattled Lapwing *Vanellus indicus*	Tiger cub (*Panthera tigris*), humans	Unpalatable	Cott, 1946
Common Murre *Uria aalge*	Humans	Unpalatable	Simon, 1944; Cott, 1946
Thick-billed Murre *Uria lomvia*	Humans	Unpalatable	Simon, 1944; Cott, 1946
Atlantic Puffin *Fratercula arctica*	Humans	Unpalatable, fishy, rank	Simon, 1944; Cott, 1946
Rueppell's Griffon *Gyps rueppellii* (listed as White-backed Vulture *Gyps rueppellii* in Cott)	Humans	Unpalatable, malodorous, dunglike smell	Cott, 1946
Red-throated Caracara *Daptrius americanus*	Hymenoptera, humans	Unpalatable, malodorous	Thiollay, 1991
Least Grebe *Tachybaptus dominicus*	Humans	Unpalatable, dark and oily	Gosse, 1847
Great Crested Grebe *Podiceps cristatus*	Humans	Unpalatable	Andersson, 1872
Anhinga *Anhinga anhinga*	Humans	Unpalatable, fishy	Wilson and Bonaparte, 1831
Turkey Vulture *Cathartes aura*	Humans	Unpalatable, malodorous, vomits carrion as defense	Wilson and Bonaparte, 1831; Cott, 1946
Great Frigatebird *Fregata minor*	Galapagos Hawk (*Buteo galapagoensis*)	Malodorous, musty smell, is avoided by hawks	D. Anderson, personal communication
Red-throated Loon *Gavia stellata*	Humans	Unpalatable, nauseating	Cott, 1946
Black-throated Loon *Gavia arctica arctica*	Humans	Unpalatable	Cott, 1946; but see Simon, 1944
Common Loon *Gavia immer*	Humans	Unpalatable, rank, fishy, dark	Wilson and Bonaparte, 1831; Selby, 1833
Antarctic Giant-Petrel *Macronectes giganteus*	Humans	Malodorous, musky scent of stomach oil	Cott, 1946
Northern Fulmar *Fulmarus glacialis*	Humans	Unpalatable, malodorous	Cott, 1946
Ifrit *Ifrita kowaldi*	Humans	Unpalatable, bitter, can cause allergic-type reaction	Majnep and Bulmer, 1977
Black-billed Magpie *Pica pica*	Humans	Unpalatable	Wood, 1862; Cott, 1946

(*continued*)

TABLE II (*Continued*)

Bird species[a]	Species for which reaction has been documented	Comments	Reference
American Crow *Corvus brachyrhynchos*	Humans	Unpalatable	Wilson and Bonaparte, 1831
Large-billed Crow *Corvus macrorhynchos*	Tiger cub, humans	Unpalatable	Cott, 1946
Black-billed Sicklebill *Epimachus albertisi*	Humans	Unpalatable, bitter	Pratt, 1906
Grey Cuckoo-shrike *Coracina caesia*	Humans	Unpalatable	Cott, 1946
Black Cuckoo-shrike *Campephaga flava*	Humans	Unpalatable	Swynnerton, 1916a; Cott,1946
Square-tailed Drongo *Dicrurus ludwigii*	Domestic cats, humans	Unpalatable, nauseating	Swynnerton, 1916b; Swynnerton, 1919; Cott, 1946
Fork-tailed Drongo *Dicrurus adsimilis*	Domestic cats, mongoose (*Herpestes edwardsii*), humans	Unpalatable, nauseating	Marshall, 1902; Swynnerton, 1916b, 1919; Cott, 1946; Barnard, 1979; Owen, 1980
Black-headed Paradise-flycatcher (*Terpsiphone rufiventer*) (presumably the Cape Paradise Flycatcher *Tchitrea perspiculata* of Cott)	Humans	Unpalatable	Cott, 1946
Red-tailed Ant-Thrush *Neocossyphus rufus*	Humans	Unpalatable, malodorous	Ziegler, 1971
Mistle Thrush *Turdus viscivorus*	Humans	Unpalatable, bitter after feeding on holly berries (*Ilex* sp.)	Cott, 1946
Southern Black-Flycatcher *Melaenornis pammelaina* (presumably the Black Flycatcher *Bradornis ater* of Cott)	Domestic cats, humans	Unpalatable	Swynnerton, 1916a,b; Cott, 1946
Black Redstart *Phoenicurus ochruros*	Sparrowhawk (*Accipter* sp.)	Unpalatable	Cott, 1946
Common Starling *Sturnus vulgaris*	Domestic cats, ferrets, raven (*Corvus* sp.), humans	Unpalatable, bitter	Macpherson, 1897; Ridgway, 1945; Cott, 1946
Eurasian Bullfinch *Pyrrhula pyrrhula*	Humans	Unpalatable, possibly toxic, bitter after feeding on berries of mountain ash (*Fraxinus excelsior*)	Naumann, 1905; Cott, 1946
Hawfinch *Coccothraustes coccothraustes*	Humans	Unpalatable, bitter after feeding on yew (*Taxus* sp.)	Cott, 1946

[a] Nomenclature and taxonomy follow that of Sibley and Monroe (1990).

More detailed descriptions (malodorous, bitter, oily, fishy, astringent, acrid, etc.) are included when they were reported. Category 1 in Table II comprises bird species for which there is experimental demonstration of unpalatability or a malodorous condition. These include the nine most unpalatable species (out of 38) from Cott's (1946) experiments and the two most unpalatable species (out of 200) from the experiments of Cott and Benson (1970). An additional 83 species have been reported by one or more authors to be unpalatable, malodorous, or to have been avoided by predators (Table II, Category 2).

For some species, the published reports of palatability vary. For example, Northern Flickers are discarded by falcons (Temple, 1994), although humans appear to relish their taste (Wilson and Bonaparte, 1831). Obviously, different predators may rank the palatability of prey differently. Alternatively, the concentration of defensive or unpalatable chemicals may vary within a species according to age, physiology, diet, genetic constitution, geographical location, and/or time of year. Such variation can lead to varying effectiveness of a chemical defense. Species with variable reports of unpalatability are noted in Table II.

The data on palatability summarized in Table II must be viewed with some skepticism. Palatability studies often evaluate species relative to other, better-tasting species. Additionally, we should expect human tastes to differ from those of natural predators. Humans may classify a species as unpalatable because its meat is coarse, oily, dark, etc., but such characteristics may not avert predators. To our knowledge, no one has tested whether such qualities as "fishiness," "oiliness," etc., correlate with palatability to natural predators. It is impossible, therefore, to evaluate the significance of reports that species such as the Black Scoter, Smew, Common Merganser, Atlantic Puffin, Least Grebe, and Common Loon taste fishy, oily, or rank. Other unpalatability data may be more reliable. For example, the Red-throated Loon is so unpalatable that it causes nausea, and Ross's Turaco, Square-tailed Drongo, and Fork-tailed Drongo have induced vomiting in humans or cats.

Twenty-two species reportedly exude unpleasant odors (Table II). The odors originate primarily from the feces, stomach oils, the uropygial and anal glands, or as a result of the digestion process. Uropygial and anal glands produce malodorous oils in the Eurasian Hoopoe, Green, Violet, and White-headed Woodhoopoe, and Common Scimitar-bill (Marshall, 1902; Jackson, 1938; Cott, 1946). Breeding female Eurasian Hoopoes and their young have an anal gland that produces a brownish secretion, which the birds can squirt at will, presumably to deter predators from the nest (Vaurie, 1973). Northern Shovelers and Common Eiders during breeding have malodorous, volatile chemicals in their feces that they spray on their eggs and nest when alarmed (Table II). It has been shown that these "nest feces," without affecting the development of the eggs, can deter rats (*Rattus* sp.), ferrets (*Mustela putoris*), foxes (*Vulpes* sp.), domestic dogs, and humans from preying upon the eggs (Swennen, 1968).

The digestive action of the Hoatzin emits an odor resembling "bad musk and ammonia" or "fresh cow dung" (Chubb, 1916). The Hoatzin is "not eaten, as far as we know, by men or animals, owing to the peculiar and unpleasant odor exhaling from the birds" (Cott, 1946). The species' flesh is palatable to humans, however, if it is carefully cleaned and cooked (Chubb, 1916; J. P. O'Neill, personal communication).

In New Guinea, the Scrubfowl and Greater Black Coucal exude nauseating odors almost immediately after death, such that the smell from a dead bird can cause humans to vomit (Diamond, 1994). Native people in New Guinea insist that these species are inedible because the birds rot almost immediately upon death. Diamond (1994) postulated that the smell may deter non-human predators as well.

4. SOURCES OF DEFENSIVE CHEMICALS

Chemically-defended species may either synthesize defensive chemicals *de novo* or obtain them from other sources. Birds can obtain defensive chemicals from at least three different sources: 1) their diet, including plants, insects, and even foods tainted with bacterial or fungal byproducts or toxins; 2) symbiotic or parasitic organisms; and 3) directly from their external environment.

4.1. *De Novo* Synthesis

The uropygial gland produces a variety of hydrocarbons, fatty acids, esters, alcohols, and other organic compounds (Jacob, 1978). Alkyl-substituted wax acids and alcohols can retard pathogenic growth of bacteria and fungi, and 3-hydroxy fatty acids are also potent fungicides (Jacob, 1978). It is possible that some constituents of uropygial secretions deter arthropod parasites as well. In addition to the uropygial gland, salivary glands, sebokeratocytes of the skin, ceruminous (wax) glands of the ear, anal (mucopolysaccharide) glands (Menon, 1984), and pigment cells (Voitkevich, 1966) also produce chemicals that may conceivably have some defensive properties.

4.2. Chemicals Sequestered from Diet

In some cases, toxicity in birds appears to result from consumption of plants that contain toxic compounds. Examples include the Eurasian Quail, already described, and the Ruffed Grouse, which eats mountain laurel (*Kalmia latifolia*, containing andromedotoxin; Bicknell, 1960). The Eurasian Quail and Ruffed Grouse have caused poisoning in humans (Wilson and Bonaparte, 1831; Bicknell, 1960; Ouzounellis, 1970; Papapetropoulos and Ouzounellis, 1978). In addition to plants, birds also eat insects or other prey that may contain defensive chemicals. Flickers and other woodpeckers eat ants (Wilson and Bonaparte, 1831; Temple, 1994), and cuckoos eat lepidopterans that contain irritant histamines (Kear, 1968). The stomach oils in procellariiforms vary across species, but the oils contain pristane, squalene, and astaxanthin, suggesting that the oil is derived from incompletely digested fish prey (Clarke and Prince, 1976).

Microbes that birds ingest may also produce toxic compounds. For example, bacteria produce the toxin responsible for botulism, and these bacteria and toxins can easily be picked up when scavenging birds eat decaying plant and animal matter.

Besides toxicity, the palatability of bird species to potential predators may also be affected by diet. Of the unpalatable birds listed in Table II, ten varied in palatability according to their diet. The malodorous condition of some bird species is also likely due to diet. Carrion feeders such as Ruepell's Griffons and Turkey Vultures obtain malodorous or unpalatable bacteria and chemicals from rotting carrion. [Turkey Vultures also vomit carrion at predators as a defense (Wilson and Bonaparte, 1831).] Vultures are notorious for their unpleasant smell and are unpalatable (Cott, 1946). The Great Spotted Woodpecker, Eurasian Green Woodpecker, and Red-tailed Ant-Thrush acquire malodorous chemicals from their insect prey (Naumann, 1905; Cott, 1946; Ziegler, 1971). The Kalij Pheasant, Tragopan, and Olive Pigeon acquire unpalatable chemicals from food plants.

4.3. Chemicals Sequestered from Symbionts

One possible example of a bird species that obtains defensive chemicals from symbiotic organisms may be the Hoatzin. Its unpleasant and musky odor is produced, in part, by the microorganisms in its digestive tract (Kirke, 1898; Chubb, 1916; Cott, 1946). Symbionts as a source of defensive chemicals are important for other taxa. Symbiotic bacteria and dinoflagellates putatively produce the neurotoxin tetrodotoxin found in some marine organisms (Yasumoto and Murata, 1993).

4.4. Chemicals Obtained Directly from the External Environment

4.4.1. Chemicals Obtained through Topical Application

As stated, birds sometimes rub ants, millipedes, lime fragments, vinegar, and other substances into their feathers. Ants produce a variety of organic defensive chemicals in addition to formic acid, including hydrocarbon chains, alcohols, citronellol, aldehydes, ketones, lactones, carboxylic acids, esters, alkaloids, and many other classes of defensive compounds (Blum, 1981; Jones *et al.*, 1991a, 1991b). Millipedes and beetles, also used in anting, produce a similarly broad list of defensive chemicals.

4.4.2. Chemicals Involved in Modification of the Nest Environment

When European Starlings collect green plant material for their nests, they choose species of plants that contain high concentrations of volatile compounds (Clark and Mason, 1985; Mason and Clark, 1986). The volatile compounds of preferred plants are mostly mono- and sesquiterpenes (Mason and Clark, 1986). One preferred plant species (rough goldenrod) contains the sesqueterpene 2-bornyl acetate and farnesol that may act as a molt-suppressing insect juvenile hormone (Rosenthal and Janzen, 1979).

5. ECOLOGY OF CHEMICAL DEFENSE

Birds serve as hosts for a number of parasites and as food for diverse predators, and it is important to consider the ecological context of chemical defenses. Although each bird species will have its own life-history and suite of predators and parasites, some generalizations can be made concerning the pressures placed upon all birds by predators and parasites.

5.1. Predators

Predators can threaten birds of all ages, but they pose the greatest threat to eggs and nestlings. Numerous species of mammals, birds, lizards, and snakes regularly include eggs and nestlings of birds in their diet, and some predators even specialize on this diet. Defensive chemicals in or on eggs, nestlings, or nests could reduce predation. A predator that found the first nestling or egg to be distasteful might leave the others alone. If the defensive chemicals were extremely potent or emitted a repulsive smell, as with nest feces of eiders, a predator might be deterred before any egg or nestling died (Swennen, 1968).

The greatest threat to adult birds comes from raptors that favor birds as prey. Because of the way raptors hunt, they have little opportunity to smell or taste prey before killing it, so gustatory and olfactory signals serve little purpose in protection against raptors. Alternatively, colors may be important aposematic signals to avian hunters. Another group of important predators of adults, at least in some areas, is specialist bird-eating snakes. Such snakes are usually arboreal, often nocturnal, and locate prey through olfactory organs and infrared receptors (Greene, 1989). Many snakes also flick their tongue toward potential prey and thus may have an opportunity equivalent to tasting prey before striking (Mushinsky, 1987). Olfactory signals could prevent initial strikes by snakes, and gustatory signals or unpalatability could cause snakes to release birds they had captured.

In some parts of the world, humans are also an important predator of adult birds. For example, in New Guinea the people regularly hunt birds of almost every species, and, for adults of species such as the cassowary (*Casuarius* spp.), humans are the only predator. The toxins of the Hooded Pitohui in Papua New Guinea are known to defend them against humans (Majnep and Bulmer, 1977; Kocher-Schmid, 1991; Diamond, 1992, 1994; Dumbacher *et al.*, 1992).

5.2. Parasites

Wild birds are hosts to a variety of ectoparasites, which can reduce growth, spread diseases or pathogenic internal parasites, and cause death. Avian ectoparasites feed on blood, skin, and/or feathers. Some ectoparasites spend parts of their life-cycle in the feathers [mites (Acarina), lice (Mallophaga), fleas (Siphonaptera), flies (Hippoboscidae)], dermis [larvae of botflies (Oestridae)], or nests of birds [mites, lice, botflies, ticks (Acarina)]. Additionally, some (e.g., ticks and lice) may be generalists that infest many avian taxa, whereas others (e.g., Mallophaga feather mites) are highly specific to certain genera or species. Specialist parasites, such as lice, often fail to be deterred by potentially defensive chemicals (Judson and Bennet, 1992; Bennett, 1994), whereas generalists, such as ticks, may be deterred, at least in the Hooded Pitohui (Mouritsen and Madsen, 1994). This may result from the nature of coevolution in host–parasite systems. Obligate single-host specialists, such as Mallophaga feather lice, may be under significantly greater pressure to evolve resistance as their host evolves chemical defenses. Generalists, in contrast, may be unable to evolve resistance to the chemical defenses of any single host species.

6. EVOLUTION OF CHEMICAL DEFENSE

Chemical defenses in birds can evolve through the same mechanisms—direct fitness benefits and natural selection—that have been documented for chemical defenses in insects (Fink and Brower, 1981; Malcolm and Brower, 1989; Denno *et al.*, 1990). If an individual bird is chemically defended in a way that protects it from predators or parasites, then it will have a selective advantage over non-defended individuals that are preyed upon or weakened by parasites. Even if defended individuals pay a cost to produce or carry the chemical, the trait should spread if the anti-predator or anti-parasite advantages outweigh the costs. In taxa other than birds, there is evidence that individuals with greater toxin concentrations have higher fitness than individuals with lower toxin concentrations (e.g., butterflies, Fink and Brower, 1981, and Malcolm and Brower, 1989; beetles, Denno *et al.*, 1990).

Apart from direct selection, animals can evolve chemical defense through two alternative ways: exaptation and kin selection. It has been suggested that preadaptation (Simpson, 1953) or, to use Gould and Vrba's (1982) term, exaptation, accounts for the evolution of chemical defense in many insects (Hay *et al.*, 1987, 1990; Brower *et al.*, 1988). An exapted trait is one that evolved to serve a particular function, yet fortuitously has, or acquires, other effects that increase fitness. For example, the use by procellariiforms of stomach oils as a food source for young birds may have evolved because of the nutritional value of the oils, and only secondarily become a defense against potential predators. Similarly, long hydrocarbon alcohols and acids in uropygial oils waterproof birds' feathers, but they also inhibit bacteria (Jacob, 1978). Many potentially defensive avian chemicals are sequestered from nutritious foods, so the defensive use of these chemicals may also represent exapted traits.

Chemical defenses may also evolve through kin selection. That is, a rare heritable chemical-defensive trait may spread even if predators kill chemically-defended individuals, provided the trait sufficiently improves the fitness of close relatives of the individual killed. If the experience of killing the chemically-defended animal is aversive for the predator, made so by the chemical, the predator may learn to avoid individuals that look like its victim (see discussions of "green beard" traits in Dawkins, 1976), and these may have a higher probability of carrying copies of genes controlling chemical defense. This potentially elevates the fitness of the victims' relatives and causes the chemically defensive trait to spread.

Gregariousness of related individuals could facilitate the evolution of chemical defenses through kin selection. Gregariousness correlates with toxicity in butterflies (Fisher, 1930; Cott, 1940; Sillén-Tullberg, 1988; Sillén-Tullberg and Leimar, 1988), whose communal groups are often comprised of related individuals. Experimental evidence indicates that predators learn to avoid gregarious noxious prey faster than solitary noxious prey (Gagliardo and Guilford, 1993), so aversive reactions that predators experience with one member of the group are likely to divert the predator from the remaining group members.

7. PHENOMENA RELATED TO CHEMICAL DEFENSE

Many aspects of morphology and behavior may relate to chemical defenses, including coloration, activity patterns, social behavior, and resemblance to heterospecifics (mimicry). Although our understanding of these correlations stems from work on taxa other than birds, consideration of them is relevant to a discussion of avian chemical defenses.

7.1. Aposematism or Warning Traits

Chemically-defended animals are often brightly colored (typically black in combination with orange, red, or yellow) or otherwise conspicuous (e.g., exhibiting slow flight, boldness, or warning displays) such that they advertise their presence. Conspicuousness of noxious prey may help predators learn to avoid them (Gittleman and Harvey, 1980; Gittleman *et al.*, 1980; Guilford, 1986; Roper and Wistow, 1986), may startle potential predators (Baker and Parker, 1979), may slow a predator's attack and thereby reduce the probability of injury to prey (Guilford, 1994), or may be innately avoided by predators (Coppinger, 1970; Smith, 1975; Schuler and Hesse, 1985; Roper and Cook, 1989; Roper, 1990; Götmark, 1994b). Aposematic coloration in insects was shown by Sillén-Tullberg (1985) to reduce predation through a combination of these effects on predators.

Some bird species known to be toxic or unpalatable have been suggested to be aposematically colored, including the brightly-colored

woodhoopoes (Marshall, 1902), the Eurasian Hoopoe (Vaurie, 1973), and the Hooded Pitohui (Diamond, 1992; see Cott, 1946 for a review of other anecdotal cases). A reanalysis (Götmark, 1994a) of Cott's studies (Cott, 1946; Cott and Benson, 1970) showed a remarkable negative correlation between conspicuousness and edibility in 38 Middle Eastern and 200 African bird species. In Götmark's reanalysis, he considered the plumage of males as well as females, controlled for variation in ranking of conspicuousness, and used appropriate statistical tests. Götmark found a negative correlation between conspicuousness and Cott's ratings of edibility in both males and females of European passerines and in African non-passerines. The negative correlation was also observed for female African passerines, but males of the same species did not show this trend. Other research has demonstrated that hawks attack some brightly-colored birds less frequently than they attack cryptically-colored birds (Götmark, 1992, 1994b, 1995; Götmark and Unger, 1994). These results suggest bright coloration may signal unpalatability in some species.

Odors, such as volatile pyrazines, may also act as aposematic warnings to predators (Guilford *et al.*, 1987). Strong odors have been reported for many toxic or unpalatable birds, including species such as the Hooded Pitohui (see Table II).

It has been suggested that many unpalatable birds have conspicuous behaviors: Eurasian Hoopoes have slow, butterfly-like flight (Vaurie, 1973); fulmars vocalize and perform a warning dance before spitting stomach oil (Swennen, 1974); and other unpalatable species move slowly, boldly, and openly (Cott, 1946).

7.2. Batesian Mimicry

In Batesian mimicry, a non-toxic or palatable species (mimic) resembles a toxic, unpalatable, or "unprofitable" species (model). A predator that has learned to avoid the model will mistakenly avoid the mimic as well. There are three suggested cases of Batesian mimicry in birds. The Red-tailed Ant-Thrush of Uganda's Bodongo forest is malodorous, presumably as a result of eating ants. The palatable Rufous Flycatcher (*Stizorhina frasero*) mimics the ant thrush nearly perfectly in appearance and behavior (Ziegler, 1971). In West Africa, Finsch's Rufous Flycatcher (*Stizorhina finshii*) mimics the White-tailed Ant-Thrush (*Neocossyphus poensis*) in similar ways. Ziegler (1971) suggested that in both examples the palatable flycatchers mimic the ant thrushes and thus escape predation; therefore, these represent cases of Batesian mimicry (see also Owen, 1980). Recently, however, some authors have incorporated the *Stizorhina* flycatchers into the genus *Neocossyphus* with the ant-thrushes (see Sibley and Monroe, 1990). If this classification is correct, then more detailed tests will be needed to distinguish between similarity resulting from mimicry and similarity resulting from shared ancestral traits.

In the Australasian archipelago, *Oriolus* orioles are sometimes suggested as Batesian mimics of *Philemon* friarbirds (Cott, 1964; Baker and Parker, 1979; Barnard, 1979). Parallel evolution of the two genera is clear (Diamond, 1982). Wallace (1863, 1869) suggested that pugnacity made the friarbirds a suitable Batesian model, but Stresemann (1914a, b) argued that bird-eating hawks rarely attack adults of large species such as friarbirds, and thus Batesian mimicry was unlikely. Cody (1973) regarded *Oriolus* and *Philemon* as "social mimics" (see Moynihan, 1968), and Diamond (1982) noted that both genera are palatable and proposed alternative social advantages for the mimicry. No critical tests of these hypotheses have been performed.

7.3. Müllerian Mimicry

In Müllerian mimicry, one toxic or unpalatable species (mimic) resembles another, but more common, toxic or unpalatable species (model). Both mimic and model benefit by sharing the cost of educating predators about their noxiousness (Müller, 1879; Swynnerton, 1916b; Sheppard *et al.*, 1985). In southern Africa, the unpalatable Southern Black Flycatcher supposedly mimics the noxious and unpalatable Fork-tailed Drongo (Swynnerton, 1916b). Because of the greater intensity of the drongo's defense, some authors cite this as an example of Batesian mimicry (Barnard, 1979; Owen, 1980). However, Swynnerton's experiments ranked the flycatcher nearly as low in palatability as the drongo, and he argued the mimicry was "for the sake of greater notoriety" (Müllerian mimicry), rather than to deceive a predator (Batesian mimicry).

It has been hypothesized (Dumbacher *et al.*, 1992; Diamond, 1992) that Variable Pitohuis are Müllerian mimics of Hooded Pitohuis in certain geographical regions. Throughout its range, the Hooded Pitohui exhibits primarily one plumage pattern. In three geographical areas the Variable Pitohui almost perfectly resembles the Hooded Pitohui, although intervening races of the Variable Pitohui look strikingly different than Hooded Pitohuis. However, several complexities of this system need to be resolved before the issue of mimicry can be properly addressed. These include varying degrees of sympatry of the mimetic and non-mimetic races of the two species, interspecific and intraspecific variation in toxicity, and phylogenetic uncertainty about the ancestral coloration of pitohuis.

Character convergence, which is common in mixed-species flocks (Moynihan, 1968; Cody, 1973; Diamond, 1987), might also represent cases of Batesian or Müllerian mimicry (Barnard, 1979; Diamond, 1992). Studies of mixed-species flocks in New Guinea have shown that five of six so called "leader species" are pitohuis (Diamond, 1987), four known to carry toxins. The leader species forage in conspecific groups but often are joined by other species, including the Black-billed Sicklebill (which is unpalatable according to Pratt, 1906), additional birds of paradise, and two drongo species. Diamond (1987) also noted that flock members share similar black and brown coloration, which suggests mimicry (Fisher, 1927, 1930; Barnard, 1979).

7.4. Gregarious Behavior

Gregariousness, or sociality, often correlates with chemical defense in insects (Fisher, 1930; Edmunds, 1974; Sillén-Tullberg *et al.*, 1982). Hypotheses related to this correlation include the possibility that sociality may encourage the initial evolution of chemical defenses by kin selection (Fisher, 1930; Guilford, 1985), that gregariousness enhances the effectiveness of an aposematic signal (Gagliardo and Guilford, 1993), and that gregariousness itself acts as an aposematic signal (Cott, 1946). It is also possible, however, that chemically-defended prey, freed from the constraint of a cryptic, solitary life because they are well defended, become gregarious for reasons unrelated to chemical defense (Turner, 1975; Sillén-Tullberg, 1988).

Many unpalatable bird species are gregarious or live in family groups. Both the Smooth-billed Ani and Guira Cuckoo have social nesting habits (Davis, 1942). In a speculative way, Brown (1974) reiterated Fisher's suggestion (Fisher, 1930) that chemical protection could promote the evolution of sociality, and hypothesized that the ani may be an example.

8. SUMMARY

Chemical defense in birds is a widespread phenomenon that has been under-appreciated and under-studied. Avian chemical defense occurs through the use of toxic and/or unpalatable compounds. Toxic compounds are chemicals capable of physically or physiologically harming target organisms. Unpalatable compounds are innocuous substances that cause an aversive reaction in target individuals.

Toxic compounds may be present in bird tissues or may be topically applied, making the individual bird the toxic agent. Although the number of toxic bird species is relatively low, evidence suggests that toxicity represents an evolved adaptive strategy against predation. Toxic birds presumably either sequester toxic chemicals from their diet or synthesize the chemicals themselves. Chemical defense through topical application involves species that preen or wash themselves with substances, and species known or believed to contain chemicals that reduce parasite infestations. Topical application involves behavioral application of substances encountered in the environment and presumably represents an adaptation against parasites. Toxic compounds may also be used behaviorally. In modification of the nest environment, nesting birds preferentially incorporate into their nests green vegetation that produces volatile chemicals capable of reducing microbial growth and inhibiting populations of parasites. This type of chemical defense appears to represent an adaptation that increases hatching success of eggs, increases nestling growth, and enhances survivorship. Birds may also use chemicals maleficently to damage or otherwise harm target organisms.

Unpalatable species are those containing harmless chemicals that make the bird distasteful, malodorous, or otherwise unpleasant. A malodorous condition may, in fact, signal unpalatability in these species. Unpalatability arises almost certainly because of chemicals sequestered from an individual's diet. A large number of species are reported to be unpalatable, but many of these reports require confirmation from field observations.

Much of the data and many of the examples of avian chemical defense we have presented are circumstantial in nature or based on anecdotal reports. Furthermore, the ecological dynamics and evolution of chemical defenses may vary profoundly according to the class of defensive compounds used (toxic vs. unpalatable) and the location of the defensive compounds. Nevertheless, the number of examples that have been quantitatively and experimentally demonstrated makes it clear that chemical defenses are important for many species of birds and that many aspects of the biology of birds should be re-examined in light of potential correlates with defensive chemicals.

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CHAPTER 5

PAST AND CURRENT ATTEMPTS TO EVALUATE THE ROLE OF BIRDS AS PREDATORS OF INSECT PESTS IN TEMPERATE AGRICULTURE

DAVID A. KIRK, MATTHEW D. EVENDEN, and PIERRE MINEAU

> *In New England they once thought blackbirds useless, and mischievous to the corn. They made efforts to destroy them. The consequence was, the blackbirds were diminished; but a kind of worm, which devoured their grass, and which the blackbirds used to feed on, increased prodigiously . . . . they wished again for their blackbirds.*
>
> —Benjamin Franklin, 1749,
> cited in Glacken, 1967

> *Birds hunting insects and worms in an orchard may not buzz so much as the proverbial bee, but just the same they are mighty busy.*
>
> —W. L. McAtee, 1921

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