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MIMICRY OF FRIARBIRDS BY ORIOLES

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ABSTRACT.—Friarbirds and orioles show striking but parallel geographic variation in plumage on islands of the Australian region, such that their populations on the same island are often closely similar in plumage. This parallelism involves mimicry of friarbirds by orioles, which are in turn mimicked by a smaller honeyeater. The larger the friarbird compared to the oriole, the more perfect is the mimicry. Friarbirds and orioles are convergently similar in ecology and morphology and belong to a guild of birds that feed together in fruiting and flowering trees and that display much aggression toward each other. Within this guild, mimics are spared from attack by larger models, which attack other smaller species. Other possibly similar cases exist among tropical birds. *Received 5 January 1981, Accepted 2 September 1981.*

BIOLOGICAL mimicry involves three roles: a mimic, which resembles another species and thereby gains some advantage for itself; a model, which is imitated by the mimic; and a signal receiver, which mistakes the mimic for the model and thereby becomes the victim of the mimic's deception (Wickler 1968). Mimicry may be visual, acoustic, chemical, or behavioral. Familiar examples of visual mimicry include nonpoisonous butterflies or snakes that have evolved to resemble poisonous butterflies or snakes in order to gain the advantage of being avoided by predators. Although many bird species are famous as vocal mimics, there are few well-established cases of visual mimicry in birds.

Over a century ago Wallace (1863, 1869: 305) described what he claimed to be an example of visual mimicry in birds, involving Old World orioles (genus *Oriolus*, family Oriolidae) and friarbirds (genus *Philemon*, family Meliphagidae) in the Australian region. Wallace's claim was disputed by Stresemann (1914a), however, and there has been no further study of this case. The present paper is based on study of specimens of all species of orioles and friarbirds and on field studies of a coexisting mimic oriole and friarbird (New Guinea), two

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Frontispiece. Adult plumages of friarbirds and orioles. Large capital letters are island names, small letters are taxon names. Top row right: a typical oriole outside the range of friarbirds (*Oriolus oriolus*). Top row left: a typical friarbird outside the range of orioles (*Philemon cockerelli*). Top row center: on the Lesser Sunda Islands an oriole larger than the *O.* [*bouroensis*] superspecies and of typical *Oriolus* plumage, *O. chinensis*, coexists with the westernmost member of the *P.* [*moluccensis*] superspecies, *P. buceroides*. Rows 2–6: coexisting friarbirds of the *P.* [*moluccensis*] superspecies and orioles of the *O.* [*bouroensis*] superspecies. The oriole mimics the sympatric friarbird to varying degrees correlated with the friarbird's size: Australia and Timor have the smallest friarbirds, and the two Australian oriole species and the male oriole of Timor are not mimics, while the largest friarbird (that of Ceram) is mimicked almost perfectly. *Pycnopygius stictocephalus* is a smaller honeyeater that mimics the New Guinea oriole. See Table 1 for details. Painted by H. L. Jones from specimens in the American Museum of Natural History.


UMBOI
LESSER SUNDAS
EURASIA
P. cockerelli
P. buceroides neglectus
O. chinensis
O. oriolus
CERAM
HALMAHERA
P. subcorniculatus
O. forsteni
P. fuscicapillus
O. phaeochromu
BURU
P. m. moluccensis
O. b. bouroensis
P. m. timorlaoensis
TENIMBAR
O. b. decipiens
WETAR
P. b. pallidiceps
O. v. finschi
TIMOR
♀
♂
P. b. buceroides
O. v. viridifuscus
P. novaeguineae jobiensis
NEW GUINEA
O. szalayi
Pycnopygius stictocephalus
P. novaeguineae yorki
O. flavocinctus
O. sagittatus
AUSTRALIA
HLJones

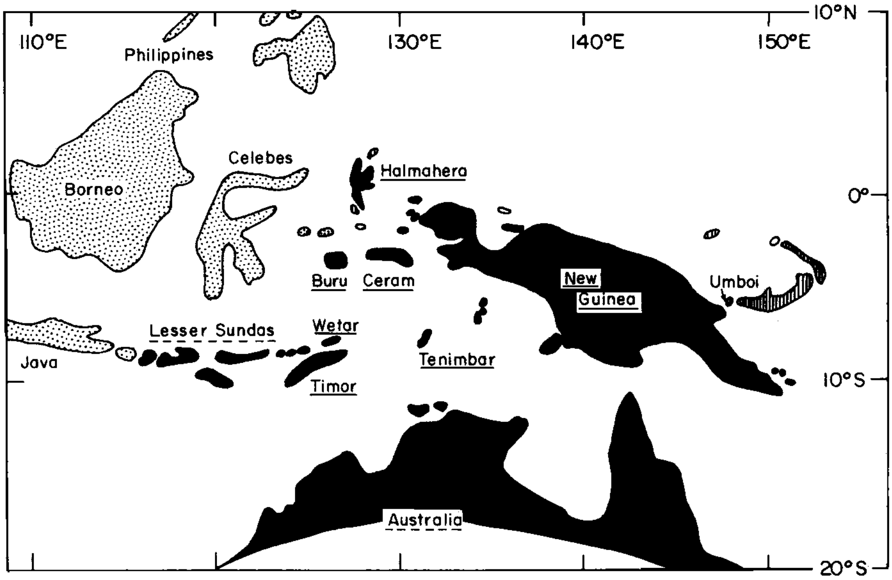

Fig. 1. Map illustrating overlap of orioles and friarbirds. Dots: *Oriolus* but no *Philemon* present. Vertical hatching: *Philemon* but no *Oriolus* present. Solid shading: both *Philemon* and *Oriolus* present; solid underlining of island name indicates mimic oriole, dashed underlining indicates nonmimic oriole. Blank: neither *Philemon* nor *Oriolus* present.

pairs of coexisting nonmimic orioles and friarbirds (Australia), friarbirds living outside the range of orioles (New Britain, Umboi), and orioles living outside the range of friarbirds (Java, South Africa, Germany).

STUDY MATERIAL AND STUDY SITES

At the American Museum of Natural History, British Museum (Natural History), and Museum Zoologicum Bogoriense I examined all specimens of friarbirds, all specimens of orioles of the Australian region (including Wallacea), and selected specimens of all extralimital oriole species.

Field observations covered the following areas and species. New Guinea (Fly River, Oriomo River, Karimui Basin, Astrolobe Bay, Huon Gulf, Torricelli and Bewani mountains, Meervlakte, van Rees Mountains, Gauttier Mountains, Onin Peninsula, and vicinities of Port Moresby, Popondetta, Wewak, Vanimo, and Jayapura): *Oriolus szalayi, Philemon novaeguineae, P. corniculatus, P. citreogularis, P. meyeri,* and *Pycnopygius stictocephalus*; Australia (Atherton Tableland and vicinities of Canberra, Sydney, Brisbane, and Cairns): *O. sagittatus, O. flavocinctus, Philemon novaeguineae, P. corniculatus, P. citreogularis*; New Britain (Cape Gloucester) and Umboi: *P. cockerelli*; Java (Bogor): *O. chinensis*; South Africa (Kruger Park): *O. larvatus*; Germany: *O. oriolus*.

Observations in the Australian region totalled 25.5 months, distributed over all months of the year and over 9 yr from 1964 to 1981.

PATTERNS OF MIMICRY

The Meliphagidae, or honeyeaters, originated and (like marsupials) underwent an adaptive radiation in the Australian region and produced the morphological and ecological equivalents of numerous families elsewhere (Keast 1976). Friarbirds, the largest meliphagids, are convergent on the predominantly Afro-Asian *Oriolus* in size, diet (nectar, insects, soft fruit), nest (woven suspended cup), and habitat (tree canopy). In adult plumage the Afro-Asian orioles are mainly yellow and black (Frontispiece: right-most two birds of top row), very unlike the mainly brown friarbirds.

One species group of *Oriolus* has invaded and differentiated in the Australian region, so that the orioles of the *Oriolus* [*bouroensis*] superspecies and friarbirds of the *Philemon* [*moluccensis*] superspecies now share eight islands or island groups. These are Ceram, Halmahera, Buru, Tenimbar, Wetar, Timor, New Guinea and neighboring islands (Waigeu, Salawati, Batanta, Misol, Japen, Aru), and north-

TABLE 1. Adult plumage of coexisting friarbirds *Philemon* [*moluccensis*])[a] and orioles (*Oriolus* [*bouroensis*]).[b]

CERAM. *P. subcorniculatus.* Olive-brown dorsally, yellow-brown ventrally, breast and axillaries yellow. Head markings: grey color; streaked crown; small bare or sparsely feathered circumocular patch. *O. forsteni.* Same. **Virtually identical.**[c]

HALMAHERA. *P. fuscicapillus.* Medium-dark brown, darker dorsally; the darkest population. No streaks and no markings except for small bare circumocular patch and slightly grey throat; the most uniformly colored population. *O. phaeochromus.* Same, except: slightly darker ventrally, throat not greyer, lacks circumocular patch. **Closely similar**.

BURU. *P. m. moluccensis.* Body as on Halmahera, except paler. Head markings: pale hind-collar, superciliary, and throat; streaked crown and throat; bare black facial patch. *O. b. bouroensis.* Same, except: has black feathered patch corresponding to bare skin of friarbird; side of throat streakier. **Closely similar**.

TENIMBAR. *P. moluccensis timorlaoensis.* As on Buru, except: lacks pale superciliary; obscure dark ear-coverts and moustache. *O. bouroensis decipiens.* Same, except: has black feathered patch corresponding to bare black skin of friarbird; crown slightly streakier. **Closely similar.**

WETAR. *P. buceroides pallidiceps.* As on Buru, except: paler brown; throat paler, almost white; bare black facial patch larger; has bare black patch on side of neck; has black moustache feathering adjacent to bare black facial skin; has bill knob. This population and the Timor one are the palest populations. They are also the ones with the boldest facial pattern, due to the contrast between the black facial skin and moustache and the whitish throat. *O. viridifuscus finschi.* Female same, except: has black feathered patch corresponding to patches of bare black skin of friarbird; streakier crown and nape; lacks bill knob. Male as female but slightly darker, upper back and crown greyer, head pattern more obscure. **Quite similar** (female), **somewhat similar** (male).

TIMOR. *P. b. buceroides.* As on Wetar. *O. v. viridifuscus.* Female same, except: has black feathered patch corresponding to patches of bare black skin of friarbird; lacks bill knob. Male different (brown lower back and belly, dull green upper back, grey breast and throat, red bill). **Quite similar** (female), **dissimilar** (male).

NEW GUINEA. *P. novaeguineae.* As on Buru, except: bare black facial patch larger; some populations have bill knob; lacks pale hind-collar and superciliary. *O. szalayi.* Similar, but plumage streaky; has streaked black feathered patch corresponding to bare black skin of friarbird; lacks bill knob; bill red (adult only). **Quite similar**. *Pycnopygius stictocephalus.* Similar to oriole, except: body not streaky; crown streaked charcoal brown and white, instead of charcoal brown and light brown; has white malar streak; bill black. **Quite similar** (to oriole).

TABLE 1. Continued.

AUSTRALIA. *P. buceroides* and *P. novaeguineae.* As on New Guinea. *O. flavocinctus* (streaky yellow-green, with black in wing and tail) and *O. sagittatus* (olive back, streaked on white below) dissimilar. **Dissimilar**.

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[a] Friarbird populations are described with respect to those of other islands, to illustrate geographic variation.

[b] Oriole populations are described with respect to the friarbird of the same island, to illustrate mimicry.

[c] The words in boldface summarize the closeness of mimicry.

ern Australia (see Fig. 1). From island to island these orioles show great geographic variation in plumage, and so do the friarbirds. Some are nearly uniform brown, others paler ventrally; darkness of coloration varies; pale complete or partial collars, dark ear coverts, dark moustache stripes, pale superciliary stripes, streaked crowns and throats, and olive or yellow washes may be present or absent; and one or more black patches of varying sizes, consisting either of bare skin (*Philemon*) or of solid feathering or streaked feathering (*Oriolus*), occur on various parts of the head (Frontispiece, Table 1). This geographic variation is largely parallel, however, such that on all islands except Australia the oriole and friarbird resemble each other, often to such a stunning degree that specimens held in the hand can be distinguished only with difficulty (and were sometimes misdescribed by taxonomists and mislabelled in museum collections). At least on New Guinea (my observations) and Buru (Wallace 1863, 1869: 305), this similarity in plumage is reinforced by similarities in posture, movements, and flight, so that the oriole and friarbird are even harder to distinguish in the field than one would infer from dead specimens. The oriole and friarbird of New Guinea are among the less closely matched mimic/model pairs in the hand. Yet the result of their behavioral similarity, added to their plumage resemblance, is that not only western ornithologists but also New Guinea hunters and gatherers who are expert at field identification of birds often confuse the New Guinea oriole and friarbird. Other field observers have commented on the difficulty of distinguishing orioles from friarbirds on Ceram, Timor, and Tenimbar (Forbes 1885: 421, Stresemann 1914b).

The visual resemblance is reinforced by vocal mimicry (New Guinea, Buru) and possibly by interspecific duetting (New Guinea, Ceram).

Several facts make clear that the detailed similarity of plumage involves mimicry of friarbirds by orioles rather than mimicry of orioles by friarbirds or convergence of each on the other. The predominantly brown plumage of the *P.* [*moluccensis*] forms is shared by all other *Philemon* species and many other meliphagids, whereas the brown plumage of the *O.* [*bouroensis*] forms is unique within the family Oriolidae. Within the *O.* [*bouroensis*] superspecies the form most similar to the typical yellow and black orioles of Asia and Africa is the most remote geographically, the nonmimic *O. flavocinctus* of Australia. The patches of bare black facial skin in the *P.* [*moluccensis*] forms are also shared by all but one other *Philemon* species and many other meliphagids, while the black feathering that duplicates this skin in *O.* [*bouroensis*] forms lacks a close parallel in the Oriolidae. *O.* [*bouroensis*] is virtually confined to islands shared with *P.* [*moluccensis*] (the sole exception is a race of the nonmimic *O. flavocinctus* on the Southwest Islands). In contrast, *P.* [*moluccensis*] occurs on at least 24 islands not shared with *O.* [*bouroensis*], and some of these populations are identical in plumage to populations on islands shared with *O.* [*bouroensis*]. Evidently, coexistence with orioles has not resulted in a modification of plumage in *P.* [*moluccensis*], whereas most *O.* [*bouroensis*] populations have diverged from their presumed ancestral plumage to mimic the local population of *P.* [*moluccensis*].

Among sympatric friarbird and oriole populations, mimicry varies from nearly perfect to nonexistent. The details of this variation are significant:

(1) There are six species or superspecies of friarbirds, all sympatric with *O.* [*bouroensis*]: *P.* [*moluccensis*] (species listed in Table 1 plus *cockerelli, eichhorni,* and *albitorques*), *P.* [*corniculatus*] (species *corniculatus* and *diemenensis*), *P. argenticeps*, *P.* [*citreogularis*] (species *citreogularis, brassi,* and *inornatus*), *P. meyeri*, and *P. gilolensis*, listed here in descending sequence of size. Only *P.* [*moluccensis*] equals or exceeds *O.* [*bouroensis*] in weight, and only it serves as a model for mimicry, even though the mimic orioles of New Guinea, Halmahera, and Timor coexist with, respectively, four, one, and one other friarbird species besides *P.* [*moluccensis*].

(2) Weight variation is slight between *O.* [*bouroensis*] populations but over twofold between *P.* [*moluccensis*] populations (population means 94–109 g for orioles, 95–194 g for friarbirds). The greater the size advantage of the friarbird over the sympatric oriole, the more perfect is the mimicry of the friarbird's plumage by the oriole. Thus, on Ceram, which has the *P.* [*moluccensis*] population with the largest body size (mean weight 194 g, 78% heavier than the Ceram oriole), the oriole is virtually a perfect mimic; on Halmahera, Buru, and Tenimbar, where the weight advantage is about 50%, the mimicry is close but not perfect; on New Guinea and Wetar, weight advantage about 39%, mimicry fair; on Timor, weight advantage 13%, mimicry fair in female oriole, absent in male; and in Australia, weight advantage about 12% (average for *Philemon* populations *gordoni, ammitophila,* and *yorki* vs. *O. flavocinctus* and *O. sagittatus*), no mimicry. Note the paradox: the more *dissimilar* the size of the oriole and friarbird, the more *similar* the plumage.

(3) A larger oriole of a superspecies different from *O.* [*bouroensis*], *O. chinensis broderipi*, coexists on seven islands of the Lesser Sundas (Lombok through Sumba and Alor) with the westernmost friarbird, *P. buceroides* of the *P.* [*moluccensis*] superspecies (Frontispiece, top row, central two birds). This oriole is yellow and black like most Afro-Asian orioles and totally unlike the brown *P. buceroides*, although the next two islands to the east of Alor (Wetar and Timor) are shared by *P. buceroides* and the smaller *O.* [*bouroensis*], and the smaller orioles do mimic *P. buceroides*.

(4) The New Guinea oriole *O. szalayi* (102 g), which mimics the large New Guinea friarbird *P. novaeguineae* (135 g), is in turn mimicked both in plumage and vocally by a smaller honeyeater, *Pycnopygius stictocephalus* (43 g).

Thus, these cases all conform to a pattern of smaller birds mimicking larger birds.

Possible Explanations of Mimicry in Orioles and Friarbirds

What is the selective advantage responsible for the evolution of this size-related mimicry? Five relevant published theories are as follows.

(1) Stresemann (1914a) dismissed the resemblances as a coincidence due to parallel evolution of orioles and friarbirds in the same environments, such as evolution of darker forms in wetter climates (Gloger's rule). Of the eight islands shared by *O.* [*bouroensis*] and *P.* [*moluccensis*], seven have elevations exceeding 1,400 m, while one (Tenimbar) is a low coral island. Annual rainfall in the lowlands, where orioles and friarbirds live, is 200 cm or higher on New Guinea, Halmahera, Ceram, and Buru, lower on Timor, Wetar, and Tenimbar, and lowest (down to 60 cm) in some areas of Australia occupied by these species. Stresemann's explanation could perhaps contribute to an understanding of interisland differences in overall darkness of plumage, though the correlation is quite imperfect: the palest forms are on two of the drier islands (Wetar and Timor), but the New Guinea forms are as pale as or paler than those on much drier Tenimbar, and the driest environment (Australia) has one of the palest *P.* [*moluccensis*] forms but the most colorful *O.* [*bouroensis*] form. Apart from these doubtful correlations between aridity and paleness, the detailed similarities in head patterns of orioles and friarbirds, and the correlation between degree of mimicry and size, make an explanation based on coincidence implausible.

(2) Cody (1969) described numerous instances in which unrelated but ecologically similar bird species converge on each other and thereby can more readily maintain interspecific territories. The mimics and models of New Guinea, Timor, and Tenimbar and the nonmimic orioles and friarbirds of Australia, however, are neither interspecifically nor intraspecifically territorial. I often observed *P. novaeguineae*, *O. szalayi*, and *Pycnopygius stictocephalus* feeding and singing together in the same tree and up to 10 individuals of *P. novaeguineae* singing simultaneously in the same tree. Finally, the oriole-friarbird case does not involve convergence (evolution of two taxa toward each other), as in the cases discussed by Cody, but mimicry (evolution of orioles toward friarbirds, without evolution of friarbirds toward orioles).

(3) Moynihan (1968) has noted numerous instances wherein neotropical bird species that habitually travel together in foraging flocks resemble each other. He postulated that this resemblance contributes to flock cohesion. On both New Guinea (pers. obs.) and Buru (Stresemann 1914a), however, the mimics and models never travel together, even when feeding in the same tree; they fly in and out independently.

(4) Is it possible that friarbirds are distasteful and that orioles are Batesian mimics? This seems unlikely, because New Guinea men working with me broiled and ate without objection several dozen friarbirds and orioles, although they did object to the taste of certain other bird species (e.g. *Megapodius freycinet*, *Centropus menbeki*). In addition, if friarbirds were distasteful and orioles not distasteful, it would remain a puzzle why *Pycnopygius stictocephalus* mimics an oriole.

(5) Wallace (1863, 1869) suggested that orioles mimic the larger, pugnacious friarbirds to escape attack by hawks. Stresemann (1914a, b) found bird-eating hawks so rare on Buru and Ceram that he considered this explanation absurd. I draw the same conclusion for New Guinea. In the New Guinea lowlands there are few widespread species of hawks likely to attack adult birds, and most of them are very uncommon or rare. Only once did I see a bird-eating hawk (the uncommon *Megatriorchis doriae*) near a tree frequented by orioles, friarbirds, and other honeyeaters, and I never saw a hawk attack a bird in such a tree.

Nevertheless, one can observe attacks *among* orioles, friarbirds, and other honeyeater species dozens of times daily, and these attacks provide a strong and obvious selective force for evolution of size-related mimicry. Orioles, friarbirds, and *Pycnopygius stictocephalus* regularly occur together, often in the same tree, because they and other honeyeaters belong to a guild of bird species that gather in flowering and fruiting trees to feed. The three New Guinea species have largely coincident habitat preferences (forest edge, clearings with scattered trees, occasionally forest), perch height ranges (canopy down to about 10 m), and altitude ranges (*P. novaeguineae* and *O. szalayi* from 0 up to 600–900 m, occasionally higher in disturbed areas; *Pycnopygius stictocephalus* up to 400–600 m). The same holds for the mimic orioles and friarbirds of Ceram and Buru. Orioles, friarbirds, and *Pycnopygius stictocephalus* also show broad overlap in their diets of fruit, insects, and nectar, although there are quantitative differences in diet (possibly related to differences in bill shape) that make coexistence ecologically possible (e.g. analyses of stomach contents by me and other collectors yielded: 72 *P. novaeguineae,* insects in 33%, fruit in 67%; 20 *O. szalayi,* insects in 10%, fruit in 90%; nectar not detectable in stomach).

There have been numerous studies of this guild of fruiting and flowering tree specialists in New Guinea (e.g. Mayr and Rand 1937; Ripley 1959, 1964; Terborgh and Diamond 1970; Beehler 1980; Pratt in press). The latter three studies included systematic measurement of bird usage and of interspecific and intraspecific aggression in the trees. Every one of these studies stressed the high frequency of fighting among guild members gathered in trees to feed. The size sequence of bird consumers defines a dominance hierarchy: large species often drive smaller species away from food resources. The fighting is adaptive, in the sense that each species devotes time and energy to driving off only those other species that overlap with it in diet and that are not larger (hence can be safely attacked). Beehler (1980: 516) describes these New Guinea feeding assemblages as "veritable riots of interindividual aggression. In general, the organizing factor among the New Guinea birds seemed to be dominance hierarchy, based on size and aggressiveness. The larger species were usually more successful; thus, they occupied the favored feeding spots with minimum harassment. But, even under the best of circumstances, the dominant species in a tree spent most of the time supplanting and chasing conspecifics and smaller heterospecifics." Pratt (in press) tabulated attacks by color-banded frugivores on other birds in fruiting trees; the attackers regularly succeeded in chasing off other birds that were not too large.

As an illustration of the adaptiveness of fighting, consider the following case involving *Pycnopygius stictocephalus,* as it has been the subject of many fewer published studies than the more common *P. novaeguineae* or *O. szalayi.* In a fruiting tree at Sogeri (450 m, southeast New Guinea), which I observed for a total of 4.5 h on 6–7 September 1979, *Pycnopygius stictocephalus* repeatedly and so successfully drove off four species overlapping with it in diet (the similar-sized cuckoo-shrike *Coracina papuensis* and the smaller honeyeaters *Meliphaga flavescens, Myzomela obscura,* and *Myzomela adolphinae*) that they could barely alight in the tree before being attacked; the three honeyeaters spent most of this time in another tree only 5 m away. At the same time *Pycnopygius stictocephalus* was ignoring five species with quite different diets (the similar-sized kingfisher *Halcyon sancta* and whistler *Colluricincla harmonica* and the smaller warbler *Gerygone olivacea,* flycatcher *Myiagra rubecula,* and mistletoe-bird *Dicaeum pectorale*), as well as five larger species that do overlap with it in diet (*O. szalayi, P. novaeguineae,* the figbird *Sphecotheres vieilloti,* pigeon *Ptilinopus iozonus,* and bowerbird *Chlamydera cerviniventris*).

On each island shared by *P.* [*moluccensis*] and *O.* [*bouroensis*], *P.* [*moluccensis*] is the largest member of the guild, and *O.* [*bouroensis*] is the second largest, while *Pycnopygius stictocephalus* is the third largest on New Guinea. Virtually all authors who have commented on the habits of friarbirds emphasize their pugnacity in driving off other birds (see e.g. Hill 1967, Bell 1969, Frith 1976, Peckover and Filewood 1976, and Pizzey 1980 for *P. novaeguineae,* and Wallace 1863; Layard and Layard 1882; Siebers 1930; Ripley 1959; Rand and Gilliard 1967; Hill 1967; Frith 1969, 1976; Pizzey 1980; and Stokes 1980 for *P. moluccensis, P. corniculatus, P. citreogularis, P. diemenensis, P. gilolensis,* and *P. meyeri*). Although I too often saw *P. novaeguineae,* as well as *O. szalayi* and *Pycnopygius stictocephalus,* driving off smaller species, it is remarkable that I never saw *P. novaeguineae* attack the smaller *O. szalayi,* nor *O. szalayi* attack the smaller *Pycnopygius stictocephalus.* This is despite the fact that I looked particularly for such an interaction during a total of about 500 h of observation at fruiting and flowering trees, spread over 19 months of fieldwork in many different areas of New Guinea, where these three species were common and observed daily. These species regularly shared the same feeding trees with each other, foraged within 1–2 m of each other, and attacked other species frequently, but ignored each other. In contrast, in northeast Australia, where the nonmimic *O. flavocinctus* meets the southern edge of the range of the somewhat larger *P. novaeguineae,* I did observe the friarbird attack and drive off the oriole. [These attacks may not interfere seriously with the oriole, because this friarbird is considerably less common than the oriole in northeast Australia and differs somewhat in preferred foraging stratum and diet, whereas in New Guinea *P. novaeguineae* is more common than its mimic *O. szalayi,* which is in turn more common than its mimic *Pycnopygius stictocephalus.* The Australian orioles may instead be mimics of figbirds (Beland 1977)]. In southeast Australia, where the nonmimic *O. sagittatus* broadly shares its range with the similar-sized friarbird *P. corniculatus,* the oriole stands its ground when attacked by the friarbird, and sometimes the oriole is the aggressor and attacks the friarbird.

It seems clear, then, that mimicry serves at least one purpose and possibly two. First, mimics escape attack by larger model species that might otherwise drive them off. It remains unclear, however, just why the model refrains from attacking the mimic. It may be that the model regards conspecifics as equal opponents and hence more dangerous to attack than smaller birds recognized as heterospecific. Both friarbirds and orioles often tolerate conspecifics in the vicinity. Nevertheless, attacks on conspecifics do sometimes occur, and one might thus expect mimics to enjoy only partial rather than nearly complete immunity. A clue to this puzzle is that *O. szalayi* is more similar to juvenile than to adult *P. novaeguineae,* because juveniles are more streaked and lack a bill knob, and that the black bill of *Pycnopygius stictocephalus* makes it more similar to black-billed juveniles than to red-billed adults of *O. szalayi.* Adult birds of many species are more tolerant of conspecifics in juvenal or subadult plumage than in adult plumage (Hardy 1974; Rohwer 1978; Immelmann 1980: 160 and pers. comm.; Rohwer et al. 1980). A second possible benefit of mimicry is that the mimic, by resembling a larger bird, may derive higher status in the eyes of smaller species and may succeed in scaring them off with less effort by its mere appearance.

To summarize the hypothetical evolutionary history of these species, the Afro-Asian genus *Oriolus* and the genus *Philemon* of the Australian region convergently evolved ecological and morphological similarities, although their adult plumages were quite different. One *Oriolus* stock then invaded the Australian region and encountered friarbirds. All friarbird species are notoriously belligerent. Where larger orioles encountered smaller friarbirds, the orioles were able to defend themselves and maintain their place in feeding trees. Where smaller orioles encountered larger friarbirds, however, the orioles, as the member of the feeding guild next in size to the friarbirds, were the prime target of attack by friarbirds, and this must have interfered seriously with their access to food. By converging in appearance on the larger friarbirds, the orioles reduced the risk of these attacks and may also have gained status with respect to smaller birds. The larger the size advantage of the friarbird over the oriole, the more perfect had to be the plumage resemblance of the oriole to the friarbird, as the oriole became increasingly unable to assert itself against increasingly large aggressors. (Even the largest friarbird is only 25% greater in linear dimensions than its mimic oriole, so that this size difference does not make it easy to distinguish the oriole from the friarbird, although the twofold weight difference does seal the outcome of fights.) Evolution of mimicry may have proceeded via retention of juvenal plumage as an adult: among Afro-Asian orioles, the dull, streaked juveniles are more similar than are the bright yellow and black adults to friarbirds, especially to juvenile friarbirds, which sometimes have streaks and a yellow wash.

From the perspective of biological mimicry, what is interesting in this case is that the model itself is the signal receiver: the victim of the deceit is the friarbird itself (or the oriole in the case of *Pycnopygius stictocephalus* as mimic), rather than some third species. Below I mention other suggestively similar cases.

TESTS AND UNSOLVED PROBLEMS

I believe that study of specimens and field observations in New Guinea presently warrant two conclusions. First, orioles are indeed mimics of friarbirds, as Wallace postulated over a century ago. The case for mimicry is much stronger than Wallace realized: he had seen only two of the eight sets of populations that we now know. Second, at least in New Guinea a plausible selective force is the "riots of interindividual aggression" (to use Beehler's phrase) that occur in the trees where orioles and friarbirds feed together. It is obvious, however, that a host of questions remains unsolved and that critical tests remain to be performed. Some of these are as follows:

(1) Most important, we need quantitative studies of the interactions (and noninteractions) of orioles, friarbirds, and other guild members. There are no published field observations at all from Halmahera and Wetar for these species; from Buru, Ceram, Tenimbar, and Timor, only scanty ones. Even for New Guinea and Australia, the most accessible of these eight islands, further quantitative studies are needed.

(2) I postulated that mimicry yields two distinct advantages: in reducing attacks by the larger model, and in more easily cowing smaller guild members. What is the relative importance of these two factors?

(3) How do several nonmimic orioles manage to coexist with large friarbirds (see next paragraph)? We have only scanty information for one area, northeast Australia.

Questions 2 and 3 could be approached by manipulative experiments and by natural experiments. Examples of manipulative experiments are to trap mimics, modify them to resemble models, and release them, as has been done for mimic butterflies. If one paints the bill of *Pycnopygius stictocephalus* reddish, or glues a knob onto the bill of an oriole coexisting with a friarbird whose adult but not juvenile is knob-billed, or bleaches the head pattern of *Pycnopygius* or of an oriole (cf. Rohwer 1978), does the former mimic become the subject of friarbird attacks, and do smaller guild members avoid it less than before? As one example of a natural experiment, do the mimic female and nonmimic male of *O. viridifuscus* on Timor differ in their spatial overlap with friarbirds and in the frequency with which they are attacked by friarbirds and avoided by smaller guild members? As further natural experiments, one could ask the same questions in coastal south-central New Guinea, where one mimic oriole (*O. szalayi*) and two nonmimic orioles (*O. sagittatus* and *O. flavocinctus*) coexist with one larger and three small friarbird species, and in most of New Guinea, where the mimic honeyeater *Pycnopygius stictocephalus* and the similar-sized, nonmimic honeyeater *Meliphaga flaviventer* often share feeding trees with larger orioles.

(4) The frontispiece documents plumage mimicry. I and other observers in New Guinea find orioles and friarbirds more confusingly similar in the field than one would guess from the frontispiece because of similarity in posture, movements, and flight, and Wallace made the same comment for Buru. Are mimic orioles more similar to friarbirds in these respects than are nonmimic orioles or orioles outside the range of friarbirds? How extensive is vocal mimicry, reported for New Guinea and Buru?

(5) Are there other examples of visual mimicry within the guild that includes orioles and friarbirds? Possible examples involve Australian orioles and figbirds (Beland 1977), and the New Guinea honeyeaters *Meliphaga flaviventer philemon* and *Philemon meyeri.*

OTHER POSSIBLE EXAMPLES OF SIZE-RELATED VISUAL MIMICRY IN BIRDS

Especially in the tropics, there are other suggestive cases involving larger and smaller birds that have strikingly similar plumage and that may conceivably be involved in mimicry. Previous authors have noted, and been puzzled by, several of these cases (Hall et al. 1966, Diamond 1972, Haffer 1974). My purpose in assembling the following list of such cases is to stimulate evaluation of them. This list is undoubtedly a heterogeneous one requiring case-by-case study to decide whether mimicry is involved at all and, if so, what the underlying selective force is.

Instances that involve parallel geographic variation, as in the case of *Philemon* and *Oriolus,* include the following (the larger species is named first in each case): the New Guinea birds of paradise *Parotia* [*sefilata*] and *Lophorina superba* [Diamond 1972: 313; cf. Stresemann's (1934) misidentification and subsequent description of the new *Lophorina* race *L. s. pseudoparotia*]; African bush-shrikes of genera *Malaconotus* and *Chlorophoneus* (Hall et al. 1966); the neotropical toucans *Ramphastos* [*tucanus*] and *R.* [*dicolorus*] (Haffer 1974: 252); and the neotropical cotingids *Lipaugus vociferans-L. unirufus,* tyrannids *Rhytipterna simplex-R. holerythra,* and tyrannids *Laniocera hypopyrrha-L. rufescens.* Instances not involving parallel geographic variation include: the neotropical flycatchers *Megarhynchus pitangua, Pitangus sulphuratus, P. lictor, Myiozetetes cayanensis, M. similis,* and *Conopias parva* (for illustrations see plate 19 of Ridgley 1976 or plate 28 of Meyer de Schauensee and Phelps 1978); the neotropical motmots *Baryphthengus ruficapillus* and *Electron platyrhynchum*; the neotropical icterid *Cacicus cela* and tanager *Ramphocelus passerinii*, and the icterid *C. uropygialis* and tanager *R. icteronotus*; the African drongo *Dicrurus adsimilis* and flycatcher *Melaenornis pammelaina*; the African shrike *Lanius collaris* and flycatcher *Sigelus silens*; and the Melanesian parrots *Domicella chlorocercus* and *Vini margarethae*.

Two factors make the argument that the detailed resemblance of orioles and friarbirds involves mimicry rather than coincidence a strong one: the resemblance is between taxa in two distant families, and the resemblance is maintained through parallel geographic variation of seven pairs of forms. None of the cases mentioned in the preceding paragraph is as compelling. Perhaps the most suggestive is the example involving cotingids and tyrannids, because it involves not only forms from different families but also parallel variation (in two rather than seven areas) and is further strengthened by the fact that the parallel variation involves three sets of taxa rather than just two, as with orioles and friarbirds. The examples involving bush-shrikes, birds of paradise, and toucans are strengthened by parallel geographic variation (over at least seven pairs of forms in the bush-shrikes, four in the toucans), but the forms belong to the same family (or genus in the case of the toucans). The remaining nine examples lack support from parallel geographic variation; four involve species in different families, five involve confamilial species. One could argue that the confamilial examples need not involve biological interactions: the two forms may merely have retained a pattern that is their shared inheritance. For instance, in a similar example drawn from African mammals, the resemblance between the hyaena *Hyaena hyaena* and the aardwolf *Proteles cristalus* is sometimes dismissed on these grounds. Whether the interpretation based on shared inheritance is more plausible than that based on biological interaction requires careful evaluation, based in part on whether the closeness in field characters is greater than one would expect from the closeness in genetic heritage.

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