

THE PARENTAL STRATAGEMS OF BIRDS.

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7. THE DISTRIBUTION OF DISTRACTION DISPLAYS AMONG SPECIES AND INDIVIDUALS.

The resource of simulating injury, like that of attacking an intruder at the nest or making feint of attack, is not uniformly employed by all the individuals of a species, nor consistently practised by the same individual. We have already seen that a male Slaty Antwren would sit in the nest until I had come almost within reach of him, then display upon quitting the eggs, while his mate stole away almost before I could glimpse her; yet at another nest of the same species, not over a dozen miles from the first, it was the female who sat closely and then displayed, while the male took an early and unobtrusive departure. While I studied birds at Vara Blanca, in the highlands of Costa Rica, I had many nests of the pretty Slate-throated Redstart, all in a low bank beside a path, which ran for a long distance between a pasture and the forest. All of these nests were in closely similar positions in niches in the bank, with the pasture above and behind them, the clear path below and in front, and the tangled bushes at the forest's edge on the other side of the path. This path offered an excellent stage for the injury-feigning act, and was equally available to all the redstarts nesting in the bank. Yet of seven whose nests survived until hatching, only five performed for me at one time or another, while two were never seen to display.

A bird may give a distraction display at any stage of the nesting operations, from the beginning of incubation up to, and even after, the departure of the young, and rarely even before the eggs have been laid. But the display is most often witnessed, and in its most convincing form, when the eggs are about to hatch or are hatching, and while the parents are brooding tender nestlings. Mousley (1939) concluded from studies of Wilson's Snipe and the Spotted Sandpiper that the performance "took place only at a time when a cycle of the breeding period was either just beginning or ending, i.e., the commencement of the incubation period after the laying of the eggs, and the climax of this period, when the young had appeared, or were about to appear". This certainly is not invariably true, even for these species; for Miller and Miller (1948), who studied 35 nests of the Spotted Sandpiper, witnessed the full injury-simulation display on every day of the incubation period from that of laying the second egg to that of hatching. But there was a marked

increase in the number of displays during the interval of two or three days from the hatching of the first egg to the departure of the chicks from the nest. Some birds, however, were not seen to display at any stage of the whole breeding cycle.

My Slate-throated Redstarts were somewhat more inclined to simulate injury as they began to incubate, and as the day of hatching approached, than in the middle of the period of incubation. One bird gave me a display soon after she began to incubate, but not thereafter, although she successfully raised her nestlings. A Collared Redstart, nesting in the same bank, simulated injury from three days before her eggs hatched to three days after. On many visits to numerous nests of the Orange-billed Sparrow of the lowland rain-forests, I have seen this largely terrestrial bird give a distraction display only once; this was by a female who was covering a newly hatched nestling and, after sitting until I came very near, gave an excellent demonstration. Some individuals of some species display rather consistently, at least during the few days immediately preceding and following the hatching of their eggs; the behaviour of others is less predictable. This is a phenomenon subject to endless variation.

Light has been thrown on this variability in the use of the distraction display by the observations of Pickwell (Bent 1942) on the Prairie Horned Lark. He found at one nest that the female lark would leave by fluttering over the ground as though in distress, if frightened from it within two minutes of her return after an absence; but if she had been incubating as long as five minutes she would leave the nest while the intruder was still a long way off, and as unobtrusively as possible, trying to escape being seen rather than to lead the potential enemy from the eggs by simulating injury. The simulation of distress was most frequent on very cold days, and in the dusk of early morning and evening. Unlike my Slaty Antwrens, these larks showed a complete gradation between inconspicuous departure while the approaching human was still far from the nest, and departure accompanied by the distraction display when he was almost upon it.

While birds in the most diverse families give distraction displays, the habit is by no means uniformly distributed throughout the whole avian class. Since it is not my intention to draw up at the present time an exhaustive list of the species known to use diversionary displays, in order to keep this part of our discussion from occupying too much space I shall confine it largely to birds of the Western Hemisphere, with which alone I have enjoyed wide experience in the field. Distraction displays are of frequent occurrence among ducks (Anatidae), partridges (Odontophoridae), grouse (Tetraonidae), plovers (Charadriidae), snipe and sandpipers (Scolopacidae), pigeons and doves (Columbidae), goatsuckers (Caprimulgidae), antbirds (Formicariidae), and wood warblers (Parulidae). These displays are less often seen among

grebes (Colymbidae), courlans (Aramidae), rails (Rallidae), stilts (Recurvirostridae), phalaropes (Phalaropidae), cuckoos (Cuculidae), owls (Strigidae), hawks (Falconidae), larks (Alaudidae), titmice and chickadees (Paridae), pipits (Motacillidae), and finches (Fringillidae). In the manakins (Pipridae), although I have found numerous nests of four species, I have seen only the stationary display of the Blue-capped Manakin recorded above. In the huge family of American flycatchers I have never myself witnessed a single instance of injury simulation, although I have devoted more attention to the nesting habits of flycatchers than of any other group of birds, and the only published record of this behaviour that has come to my attention is that of Russell and Woodbury (1941) for the Grey Flycatcher. In the large family of wrens (Troglodytidae) I have seen injury-simulation on a single occasion, in the Spotted-throated Wren, and I know of a single published record, that of Nice and Thomas (1948), who saw a mild form of the display in the Carolina Wren. In the troupials (Icteridae) distraction display seems confined to the largely terrestrial meadowlark *Sturnella*. Injury-simulation has been repeatedly recorded for Old World thrushes (Turdidae) but, curiously enough, apparently not for any of the numerous species confined to the Western Hemisphere. (Many of the foregoing records are from correspondence in 'The Auk' 1936, and from Nice 1943.) Distraction displays have never to my knowledge been recorded for and are doubtless absent from at least the great majority of the species in the boobies and gannets (Sulidae), cormorants (Phalacrocoracidae), kingfishers (Alcedinidae), motmots (Momotidae), hummingbirds (Trochilidae), trogons (Trogonidae), toucans (Rhamphastidae), jacamars (Galbulidae), woodpeckers (Picidae), woodhewers (Dendrocolaptidae), ovenbirds (Furnariidae), cotingas (Cotingidae), swallows (Hirundinidae), vireos (Vireonidae), honeycreepers (Coerebidae), tanagers (Thraupidae), crows and jays (Corvidae) and others.

It is revealing to consider the occurrence of distraction displays in relation to the character and site of the nest. Plovers, snipe, sandpipers, stilts, partridges, grouse, goatsuckers, larks and most ducks usually lay their eggs on the ground, in an open nest or none at all. Pigeons may build their usually frail nests on the ground, but far more commonly place them in bushes or even high up in trees. While very few of the antbirds breed upon the ground, their nests are rarely at a great height, usually within a man's reach in the forest undergrowth. Many kinds of wood warblers build on or near the ground, but others nest well up in trees; and it is of great interest to find some of these, as the Black-throated Green Warbler, the Pine Warbler, and the Yellow-throated Warbler, falling from their nests a distance of 25 feet or more to creep with drooping wings over the ground, then sometimes returning to flutter along horizontal branches near the nest. Among finches the habit of simulating injury appears to be restricted to

those species that nest on or close above the ground; while in the typically arboreal oriole family (Icteridae) it has been recorded only for the ground-nesting meadowlark. As we should expect, it is said to be rare among chickadees and titmice, which breed in cavities in trees. Injury-simulation has been recorded for the Yellow-billed Cuckoo, which constructs its slight nest in bushes or trees, usually not high above the ground. Most surprising of all, the ruse is sometimes practised by birds of prey such as the owls. The Short-eared Owl nests upon the ground; but the two other species that are known to perform, the Long-eared and the Great Horned Owls, breed in trees, often at considerable heights.

Birds which nest in burrows, including kingfishers, motmots, jacamars, and many swallows and ovenbirds, do not simulate injury nor, so far as my experience goes, make any other form of demonstration, such as darting at the intruder who disturbs their nests. Yet many of these nesters underground are most devoted parents, sometimes clinging so steadfastly to their eggs or nestlings that they may be taken in hand, while after being driven from the burrow their loud cries of distress evince their concern for their progeny. Their lack of all but vocal demonstration seems easily explained by the position of their nests. An animal digging down to the nest-chamber from above would not be likely to see the bird as it issues from the mouth of the tunnel some feet away; while if the predator crept into the burrow through its entrance the parent would be trapped. Thus distraction display by a bird that nests in a burrow would be either ineffective or impossible.

Likewise, nesters in holes in trees, termitaries, and kindred cavities—trogons, toucans, woodpeckers, woodhewers, many cotingas, and others—almost invariably fail to do anything more effective than cry out in anger or distress when their nests are threatened. Of the many kinds of woodpeckers into whose nests I have looked, only the Golden-fronted Woodpecker has darted threateningly past me; yet some of the more powerful members of the family successfully defend the gateway to their citadel with their sharp bills when invaders less formidable than man attempt to force an entry. Here, again, the usual absence of a demonstration results naturally from the position of the nest; for an animal with its head in the hole would hardly be attracted by the feints or ruses of the owners without. The same considerations apply to the closed nests of wrens and some ovenbirds. It is of great significance that birds whose low nests are placed among tangled vegetation, with no open area close by, do not often try to give a distraction display, even when they are members of species that, under more favourable conditions, do so. Birds fail to simulate injury unless they have a suitable stage.

The virtual absence of the broken-wing stratagem from families of birds whose open nests are practically never built upon the ground, including

hummingbirds, American flycatchers, honeycreepers and tanagers, suggests that among pigeons and wood warblers the habit may have arisen among ancestors that built on or near the ground, and persisted while they gradually extended their nesting higher into the trees. Flycatchers, including some of the smallest and weakest of them, often dart at an intruder and threaten with angry castanet-like snappings of their bills; while hummingbirds, honeycreepers and tanagers may sometimes attack a snake or other small assailant of their nests, but fail to demonstrate in the presence of man. Gulls, most terns, boobies, flamingos, pelicans and other species that nest in crowded colonies on or near the ground do not as a rule attempt to lure away the intruder that threatens the safety of their nests, although some—as gulls and terns—may dart at him in a most disconcerting manner. In these populous colonies the ruse might at best lead the invader from one nest to another, and would create so much disturbance in the community that whatever an individual bird might gain by it would be more than offset by the loss to the colony as a whole.

The widespread occurrence of distraction displays among pigeons is of special significance. The whiteness of the shells of the two eggs—or less often the single egg—placed upon the most open and generally frailest of nests, appears a glaring exception to the rule that eggs laid in open nests are pigmented to make them less conspicuous. But since, from the morning the first is laid, the two parent pigeons between them keep the nest almost constantly covered, the gleaming white eggs are not often exposed to view. Most pigeons that I know sit very steadfastly, leaving the nest only at the latest moment consistent with self-preservation. With them an early and inconspicuous departure would be highly imprudent, for it would leave the most conspicuous of eggs exposed to catch the prowler's eye. After the intruder has come near, the white eggs are less likely to attract attention than the movements of the departing pigeon, which makes one final attempt to draw off the enemy from its treasures by its usually proficient imitation of a wounded bird. It is of interest that the habit of displaying so persists even in a dove, *Nesopelia galapagoensis*, of the Galápagos Islands, which apparently has no native enemies and is quite fearless of man, yet performs in typical columbine style when he approaches its nest (Swarth 1935). The same considerations apply to a certain degree to goatsuckers like the Pauraque, whose eggs, although pigmented, do not blend nearly so well with the dead leaves on which they usually lie as does the plumage of the parent birds, which between the two keep them almost constantly covered, and try to lure away the intruder when they are forced to retire.

8. THE EFFECTIVENESS OF DISTRACTION DISPLAYS.

Concerning the effectiveness of injury-simulation, or even the frequency with which birds resort to it, we have all too few observations save in respect

of man and his associated animals, particularly the dog. Yet there is evidence that the ruse has been successful with animals so diverse as otters, weasels, stoats, foxes, coyotes, cats, dogs, men and larger birds, leading them away from the nest or from young that had recently departed it (Armstrong 1947: 103–105).

I have seen only a single parent-bird give a distraction display before a mammal other than a dog. In August 1947 I spent much time watching a nest of Sclater's Antbird, situated 16 inches above the ground in the forest near my house. The open, cup-like structure was placed beneath a towering mastate tree *Brosimum utile*, whose small brown fruits, thickly scattered over the surrounding ground, were attractive to Agoutis *Dasyprocta*. These big, brown, terrestrial rodents are largely, if not wholly, vegetarian; but I was told by a neighbour that one raised on a farm attacked young chickens. On the morning after the antbird's single egg hatched, an Agouti spent much time in the vicinity of the nest, where it sat on its haunches to eat the fruits or seeds, holding them, squirrel-like, in its forepaws and incessantly twitching its ears, apparently in an effort to keep off the swarms of mosquitos that constantly hovered around its head. At first the antbirds paid little attention to the rodent beyond scolding, and the latter seemed to take no notice of the nest. But when, after half an hour, the animal, coming quite close to the nest, raised its head to sniff, the male antbird, who was brooding, suddenly jumped out and flew away low above the ground. The Agouti at the same time bounded away in the same direction, although so far as I saw the bird gave no distraction display. Possibly the Agouti was merely startled by the bird's darting past it. When beyond my field of vision, the antbird scolded; but the rodent soon returned to continue eating fruits close by the nest, to which it paid no more attention. Five days later the male antbird, always more attentive to the nestling than its mother, fed and brooded it quietly while the Agouti foraged all around, sometimes coming within a yard of the sitting bird.

But when the nestling was eight days old, and its plumage just beginning to expand at the tips of its long pin-feathers, two Agoutis came together toward the nest, one approaching very near it. The male antbird, who was just then moving off after having fed the nestling, promptly returned, dropped to the ground in front of the nearer animal and fluttered as though injured, causing it to start in his direction, when he flew up out of its reach. The Agouti followed the antbird only a foot or so, then stopped and sniffed the air near the nest. Incessantly uttering his high, rattling alarm note, the antbird again and again dropped to the ground and repeated the distraction display in front of the intruder, each time inciting the animal to make a little start in his direction, but without succeeding in enticing it from the nest. These repeated demonstrations by the male antbird seemed to excite the suspicions of the Agouti. On earlier occasions when it came close and

the parents mostly ignored it, the animal, although it might sniff the air a bit, seemed not to suspect the presence of a nest. But now, after the antbird's continued demonstrations, it sniffed and sniffed, wrinkling up its broad, pink nose and moving all around the little clump of vegetation in the midst of which the nest was supported. At last it touched the nest with the tip of its snout: I violently shook the cloth of the hide from which I watched; and it bounded away, leaving the nest slightly tilted. But soon the animal returned, going so directly toward the nest that I could scarcely doubt its intention; so I burst from the front of the hide and chased it away. During this climax I did not see either of the parent birds, possibly because the rodent so thoroughly held my attention.

Before leaving at midday I propped up the leaning nest, and at dawn next morning I found the female antbird brooding her nestling. Later in the day the youngster vanished, torn from its nest, to judge by the condition in which the structure was left. Whether the Agouti or some other animal was responsible for its disappearance I could not decide. I believe that the antbird's distraction displays might have been more effective in luring away a typically carnivorous animal like a tayra or a fox than this Agouti, whose whole behaviour showed it to be at most an occasional predator—which only made the situation more perplexing for the antbird to meet, and led to results contrary to what might have been expected. Strangely enough, neither of the parent Sclater's Antbirds at this nest ever simulated injury before me on any of my numerous visits. But a year later, when there was a nest, possibly belonging to this same pair, in the same part of the forest, both parents gave convincing distraction displays in front of me, the female this time proving to be the better actor.

Years earlier, I was watching a family of Black-striped Sparrows in Vargas Park, Puerto Limón, Costa Rica. The group consisted of the parents, a fledgling just out of the nest and scarcely able to fly, and two youngsters from an earlier brood in juvenal plumage with spotted breasts. After a while a dog came along in company with a nurse-girl and a child and, espying the birds on the bare ground beneath the shrubbery, rushed at them. The fledgling was in an exposed position at a distance from cover, and I was certain that it was on the point of falling into the jaws of the dog. But, quick as a flash, one of the parents placed itself in front of the beast and, fluttering along the ground just ahead, led it rapidly away from the helpless little bird. The dog was still eagerly pursuing the parent sparrow when both passed from view amid the shrubbery.

An instance was earlier given of a Killdeer which by prompt, resolute action saved a nest from a dog, and the literature contains numerous other observations of the same type. Dogs seem rarely able to resist the attraction of a bird fluttering over the ground or flying low. I sometimes visited a Costa Rican plantation where a long, narrow grove of imported cypress

trees stood on the crest of a low hill in the midst of open pastures. Among these sombre-hued trees a number of Red-billed Pigeons built their nests, usually from eight to fifteen feet above the ground. The owner's dog would sometimes follow me on my visits to these nests. Upon my near approach to the incubating or brooding pigeons they would fly off, often skimming low over the adjoining open fields, and the dog would give chase, although the birds did not actually feign injury or even touch the ground.

The parental ruse may even be practised by a small bird in the presence of a larger, harmless one that has wandered too near its nest. Selous (1927) tells how a male Kentish Plover leads off an Oyster-catcher, "scuttling about over the ground just in front of him, with his tail spread and feathers all ruffled out. This conduct quite surprises the big bird, who makes several runs or starts at the little one almost under his feet, and then settles himself down quite near the nest when the latter desists—a fact well worthy of note, I think, for, however near, there is no danger so long as the oyster-catcher keeps where he is".

In continental areas I believe that snakes are, all in all, the most devastating of the enemies of nesting birds. I have been the distressed and unwilling spectator of a snake's raid upon a nest more often than I should have liked; yet the ill-omened nest never chanced to belong to a bird of a kind known to resort to distraction displays. If the raid occurred by day, the birds would protest with loud cries, dart at the serpent, or even seem to peck it. Contrary to a widespread popular belief, adult birds appear not to fear snakes except as enemies of their helpless progeny, and at times seem to go out of their way to molest them. Once, while bathing at evenfall in a deeply shaded tropical stream, I watched a pair of Bay Wrens attack a black snake, five or six feet long, which had climbed into the bushes overhanging the rocky channel. Boldly advancing, the little wrens pecked or bit it several times on the tail or even the middle of the body, with each attack causing it to move slightly. Yet I could not discover that they had any nest to guard in the vicinity. Nice (1939) recounts how a female Song Sparrow fought small garter-snakes and drove them from the nest; yet, strangely enough, no record of any bird employing distraction display in the presence of a snake has come to my attention. But what could the courage or the wiles of the boldest small bird avail to protect its family from these reptiles, so insensitive when ravening that they are not to be stopped by the sound of gunfire at close range, nor by bullet wounds that will soon prove mortal?

9. OTHER PARENTAL STRATAGEMS.

There is one special contingency in the life of a parent bird which we have not yet considered. We have seen that when approached by a potential enemy while sitting on the nest there are two strategically sound procedures open to

it. If, when about to return from an absence, it is aware that unfriendly eyes lurk in the vicinity, it will as a rule defer its approach, for to go to the nest in the presence of an enemy is the height of avian folly. I have spent hours and fruitless hours waiting in the tropical forest, with the best concealment that the vegetation could give me, for some small bird to return to a nest and eggs that I could not identify without seeing the owner. But suppose that the parent is surprised while standing upon the nest's rim feeding or guarding its babies. It is then, properly speaking, neither in the nest nor out of it, but in a half-way position that is peculiarly compromising. What course should it pursue? Most birds appear to make no special provision for this contingency. They either flee or remain steadfast, much as they would do if actually sitting. But obviously they are more exposed and more likely to attract attention to the nest while standing upon its rim than when crouched in its concavity.

The only bird that I have ever seen rise in a special way to meet the embarrassing situation of being discovered upon the rim of the nest is the Cedar Waxwing. Revisiting a nest I had discovered, ten feet up in a white pine tree, I happened to find one of the parent waxwings brooding the two half-grown nestlings. The other parent was resting upon the rim, standing quite erect, with bill inclined slightly upward and crest laid back. He remained motionless in this attitude as long as I cared to watch. This was not a chance pose; for on a later visit I again surprised one of the parents resting on the nest's rim in the same sentinel-like attitude. Evidently it had just flown up to feed the nestlings, for its throat appeared to be distended with food to be regurgitated for them. I decided to see how long it would continue this stiff pose; and during twenty minutes it stood immobile, save only a slight swallowing movement. Toward the end of this period its head began to sag to one side, from fatigue no doubt. Then I shook the small pine tree, causing it to vibrate to its crown; but the waxwing resolutely continued in the same attitude. Next, desiring to make still further proof of its constancy, I climbed the tree. The brave bird lingered until my head was nearly level with the nest, then flew silently away.

It seemed that the Cedar Waxwing was trying to escape detection by assuming a statuesque attitude, as bitterns and herons sometimes do. Its chance of avoiding notice, already good on the ground of immobility alone, was heightened by its stiff, erect, unbirdlike posture. Herrick (1905), who has described the same behaviour by this species, suggests that "the olive-gray, rod-like body of this bird might . . . when surrounded by foliage, have been readily mistaken for a short stub or a truncated branch of a tree".

One of the most extraordinary of parental stratagems was practised by some big cactus wrens *Heleodytes nuchalis* of the Orinoco Region while Cherrie (1916) was collecting their nest. He vividly describes their behaviour:

"A nest containing four fresh eggs was found at Caicara, May 12, 1907 . . . It was one of half a dozen irregular shapeless masses of fine soft rootlets, grasses, feathers

and tufts of the soft silky down from fruits of the silk-cotton (*balsamo*) tree. Each of the nests, apparently masses of rubbish, was provided with two or three entrances to as many chambers, or instead of opening into separate chambers they were in some cases entrances to tunnels through the nest mass! Only one of the several nest masses, however, was in use as a nest proper. That contained four fresh eggs. To the nest cavity proper there was only one entrance, but in addition there were in the same nest mass two tunnels running from side to side. At the time when the eggs were secured both parent birds were present and showed the greatest excitement. Their actions were most extraordinary, and instead of employing their time with cries of distress, or scolding the intruder, they immediately went to work, industriously carrying mouthfuls of soft feathers and *balsamo* from one nest mass to another, but not going near the real nest. However, when they realized that the enemy could not be deceived by their artifice, they turned their attention to the nest mass containing the eggs, and worked with such a will, and with such good effect, packing the entrance with *balsamo* and soft feathers, even while I was engaged in cutting the branch that supported the nest, that by the time the nest was on the ground no entrance was visible. For a moment I was inclined to believe I had made a mistake."

Another cactus wren, *Heleodytes griseus*, of the same region uses the abandoned nest of some other bird, usually the oven-shaped nest of a flycatcher. In a single isolated tree on the savannas there may be from three to eight nests of this type. The older and more dilapidated in appearance the nest, the more acceptable to the cactus wrens. They line the old nest with soft dry grasses and down from the seed-pods of the silk-cotton tree, and lay from three to five eggs. If their nest-tree is closely watched they become active in taking material into one of the newer nests, but do not approach the old one which shelters their family. Their object seems to be to divert attention from the old, apparently abandoned, structure—their true nest—by making a show of building a new one.

This is strange behaviour—a deceit that appears to call for a nicer mastery of the art of deception than birds often display. Apparently it is an example of the "false nest-building" discussed by Armstrong (1942, 1947). It is well known that when a bird's instincts are thwarted, or it has been subject to excitement of more than usual intensity, it performs acts that are obviously not purposive and frequently appear most incongruous. So after an escape from danger, or in the intervals of fighting, or while its nest is being looted, it may sing, or go through the movements of preening, feeding, or drinking. A female Yellow Bunting, after having driven an intruder from her territory, collected grass only to let it drop. Possibly the cactus wrens' curious stratagem has developed from substitute activities of this sort. We are ignorant whether it is employed in the presence of potential enemies other than man, and whether it ever actually averts destruction from the eggs and young. The interpretation of such behaviour is fraught with such great difficulties that we cannot be sure whether the wrens act with deliberate intention or merely discharge, in a manner which appears to the human watcher to be intelligent, nervous energy diverted by external influences from its normal channels.

Wrens have also been credited with another queer stratagem. It is well known that many kinds of these restless little birds build more nests than they can possibly use for raising their families; and there is a widespread belief that the extra structures serve as "dummies" to deceive predators as to the true position of the eggs and nestlings. As I have pointed out elsewhere (1940), those nests not used for reproduction are built at seasons when the wrens are not breeding, and many of them serve their makers as dormitories. It is rare to find them so placed with reference to the breeding nest that the artifice employed by the cactus wrens of the Orinoco region would catch the eye of a predator intent upon the true nest. In the present state of our knowledge both of the habits of the wrens and of the psychology of the serpents and other creatures that eat their eggs and young, we are hardly justified in holding that the construction of "dummy" nests is a stratagem whereby the birds deceive their enemies.

The expedient of covering over the eggs when the bird departs the nest is employed far more rarely than it might be. One would suppose that such a simple precaution would prevent the loss of many an egg, yet birds rarely make use of it. The habit is well developed among grebes, which carefully cover the eggs with loose materials of the nest before going off on a recess. Ducks cover their eggs with feathers or sometimes with dry leaves, partridges with grass and leaves, Kittlitz's Sand Plover and the Patagonian Seed-snipe with sand or dry earth (Armstrong 1947). The eggs of the Band-tailed Tityra, a member of the cotinga family that nests in old woodpecker-holes and similar cavities in trees, are more or less covered with dead leaves during the female bird's absences; but it is difficult to decide whether the bird makes an effort to achieve this result, or whether it is accidental, the loose litter which fills the bottom of the cavity merely flowing over the eggs as the tityra rises from them. Likewise the eggs in the bulky globular nests built in the tree-tops by the White-winged Becards are sometimes found to be covered over by the small dead leaves that form part of the lining; and here again it is impossible to decide whether this is an intentional or accidental result. During the absences of the solitary brown Northern Dendrocicla from her nest in a hollow palm-trunk or other natural cavity she leaves her two white eggs more or less completely covered by the whitish lichens that form the uppermost layer of the lining. Although at times the lichens only partly conceal the eggs, by breaking their outline they make them extremely difficult to distinguish in the dim cavity where they lie. The female Black-capped Chickadee, which nests in holes in trees, was found by Odum (1941) to cover her eggs with the lining of the nest during the period of egg-laying.

Eggs in holes and in completely enclosed nests would seem to be less in need of a protective screen than those in open nests; yet such covering might at times stand between them and destruction by a snake or nest-robbing bird. But whatever device a bird uses for the protection of its nest is

eventually cancelled by some enemy that catches on to the trick. The great fortresses of sticks that the castle-builders *Synallaxis* construct, with their long entrance-tunnels and narrow, inconspicuous entrance-ways, must have effectively guarded their eggs and nestlings in the days when such avian strongholds were new in the world, but now castle-builders seem to lose as large a proportion of their progeny as their neighbours that content themselves with simple, open nests.

Another parental stratagem may be briefly described as "shielding flight". As a fledgling takes its departure from the nest, especially if this be high and exposed, a parent will often follow it closely, usually flying above or a little behind the youngster until it comes to rest. I have witnessed such close escort of the fledgling on its earliest flight by birds so various as Montezuma Oropéndolas, Brown Jays, Rough-winged Swallows, White-backed Dippers, Inquisitive Tityras, and several kinds of American flycatchers. Danforth (1930) saw a parent Sparrow Hawk follow closely one of its young as it departed the old Flicker's hole where it was reared. The value of such a practice seems obvious. Should a predatory bird pursue parent and young flying so close together, the old bird would probably veer aside at the critical moment. The bird of prey would then in all likelihood follow the uppermost of the two, on which its eyes were fixed, giving the weakly flying fledgling a few moments' grace in which to reach shelter. Among birds more or less gregarious during the nesting season, as Oropéndolas, Brown Jays and swallows, the first flight of a fledgling may be a spectacular event, for the youngster, untried upon the wing, is often closely followed not only by its parents but also by such neighbours or helpers as happen to be close by when it leaves home.

A pair of Neotropical Kingbirds reared two fledglings in a slight, open nest built low above the water, among the tangled stems and roots of the epiphytic growths that covered over an old, partly submerged tree standing near the shore of Gatún Lake in the Panamá Canal Zone. I happened to be watching from a cayuca when the young kingbirds took their departure. Soon after sunrise the first suddenly left the nest. Directing its course to the nearest shore, about seventy-five feet distant, it flew quite well, high above the water. As soon as the parents noticed what was taking place they hurried in pursuit of the youngster, and while it was yet many feet from the shore one overtook it and flew directly above it, apparently in contact with it. The parent was certainly not in a position to support the fledgling and, if anything, forced it lower. Together parent and fledgling reached the shore, where the latter alighted in some bushes in plain sight. Immediately both parents flew at it and knocked it from its exposed perch into the midst of the foliage, where it was well concealed. The second act was commentary upon the first. They appeared to be trying to prevent the youngster from making itself conspicuous. The fluttering flight of a fledgling has a very

different aspect from the controlled flight of an adult bird, even at the same speed. A fledgling kingbird, weakly flying, would be tempting prey for a hawk which the adults, far from fearing, would only harry and mock.

A flock of black Yellow-rumped Caciques had attached their long woven pouches to the branches of an epiphytic bush growing at the top of the same decaying trunk where the kingbirds nested. About two hours after the departure of the first kingbird nestling the second decided to leave the nest. As it flew out over the water, three caciques hurried after it and one or two of them struck against it. One of the parents darted up to the rescue, and the caciques turned back to their nests. Although doubtless this fledgling was just as capable as its nest-mate of flying to the shore, the interference of the caciques caused it to fall into the water a few yards from the shore-line. I hurried to the scene in order to assist it if necessary; but before I could untie my canoe and reach the spot the little flycatcher had flapped its way to the land, where it crawled out on the sloping bank. Here the parents flew down to it and tried to coax it farther from the water.

Why did the caciques pursue the fledgling flycatcher? It could hardly have been because they bore it malice or wished to eat it—they had had ample opportunity to attack it in the nest, in the absence of its parents, had they so desired. Birds of all kinds perched among their swinging nests and provoked no enmity, unless they were the parasitic Giant Cowbirds. I think it may have been the strangeness of the flying kingbird that caused the caciques to rush in pursuit of it—its slow, fluttering flight was very different from the swift, direct flight of the adult birds which had been coming and going from the nesting colony. An alternative explanation is that the caciques were actuated by the same parental instinct to shield a fledgling on its earliest flight as caused the parent kingbirds to hurry to the first fledgling, and that the unfortunate outcome to the young kingbird was the result of the disparity between its own size and that of its would-be protectors.

Behaviour somewhat similar to that of the kingbirds who knocked their fledgling from an exposed perch has been described by Howard (1952): "Parent birds sometimes stand on the back of their young to push them from an exposed perch if a Hawk flies overhead, also, when the young are full-grown and demanding food too roughly, the parent will occasionally subdue them by standing on their backs." And later: "If the warning note to take cover from above is unheeded, the parent Great Tit sometimes pushes the fledgling from its exposed perch by kicking from above with its feet, scold-notes accompanying the push."

The bold attacks which some birds make upon those who threaten their nestlings, the buffetings and pecks and scratches and strokes of wing which the devoted parents shower upon intruders many times bigger than themselves, are beyond our present scope. A direct attack, whether frontal or from the rear, is not a stratagem. Some of the larger hawks can so maltreat a man that

it is dangerous to climb to their eyrie; and the bill of a determined domestic hen may well keep intruding hands from her nest. A bird no larger than a jay, if bold and resolute, may terrify a marauding cat, and doubtless also earns the respect of such animals as squirrels and weasels. From all that I have seen of the insensitivity to pain or fear of a snake intent upon its prey, I doubt whether any bird not powerful enough to kill or carry off the assailant could often put up an effective resistance when a fairly large one attacks its nest; but, as we earlier saw, Mrs. Nice's Song Sparrows sometimes succeeded in driving off small garter-snakes. And many small, weak birds will defy an intruding snake, as they will peck and buffet the man who touches their nest. We respect them the more for these courageous yet ineffectual attacks upon ourselves.

10. THE ORIGIN OF DISTRACTION DISPLAYS.

The first fact that demands consideration in an attempt to discover the origin of the stratagems we have been discussing is their irregular distribution among the orders, families, genera and species of birds. This is true of most of these ruses, not only of distraction displays; but since the latter, by their conspicuous and surprising character, have attracted most notice and we have far more observations on them, we shall for the present confine our attention to them. It is evident from their irregular distribution that, for a heritable character, distraction displays are either acquired or lost with comparative ease.

If we hold that such displays were practised by some form ancestral to all, or most, existing birds, then we must assume that they have been lost by practically all those groups of birds whose nests are so situated that these demonstrations could be of little service in saving the eggs or young from predators. Such loss would appear more probable if it were evident that injury-simulation and similar displays as a rule become harmful to a species when they cease to be advantageous, so that selection would tend to eliminate them. But if they failed to divert predators from the nest they would seem not to affect the welfare of the eggs or young either favourably or unfavourably; nor is it easy to see how such demonstrations can be detrimental to the adults unless they allow themselves to be caught, which seems almost never to happen. We know far too little about the relations between nesting birds and their many flightless enemies in continental areas to be able to affirm for any given species that its distraction display is always futile. But we know several instances of birds of oceanic islands devoid of terrestrial predators which still simulate injury when their nest is approached by man, as the Kerguelen Teal (Armstrong 1947) and the Galápagos Dove (Swarth 1935); and this seems to show that such displays may persist for a long time after they cease to be useful, albeit among the more conservative families of birds. On the other hand there are certain possible cases of the loss of distraction display. One of these is the Buff-rumped Warbler, of which I have studied a

number of nests without ever witnessing such a display; yet it is a member of the wood warbler family in which injury-simulation is widespread. The oven-shaped nests are built on banks, often facing a waterway, which would discourage grovelling over the ground and even make it dangerous to do so.

In families such as the finches, thrushes and troupials, of which only a small proportion of the species, chiefly those whose nests are placed low, are known to simulate injury, it seems far more probable that the exceptional species acquired such displays independently rather than that they retained them from a displaying ancestor of the family as a whole, while the majority of its members lost the habit. And if, because it makes the least assumption, we accept the hypothesis of the repeated acquisition of distraction displays, it will not be sufficient to suppose that they were acquired by a few ancestral forms from which major groups have sprung—the progenitors of the Charadriiformes and of the Passeriformes, for example—because in each of these orders there are families in which well-developed displays occur along with others from which they are absent. And, as we have seen, in a number of families there are genera which simulate injury and others which do not. Taking all the facts into consideration, I believe that the present distribution of distraction displays among the genera of birds has been brought about by the repeated independent acquisition of the habit, and its loss in certain instances. Williamson's (1952) study of regional variation in the distraction display of the Oyster-catcher shows how readily modifiable with changing conditions this sort of behaviour is, and such plasticity suggests that the display as a whole may be gained or lost with comparative ease.

If we postulate the repeated acquisition of distraction displays by birds of the most diverse affinities which have adopted nesting habits that allow them to be effective in luring away predators, it seems necessary at the same time to suppose some innate foundation for this faculty, widespread among birds, upon which slight and readily acquired genetic changes would suffice to build up the habit or bring the latent propensity into the light. Some ornithologists have, as already mentioned, seen in the clash of self-preserved and reproductive drives, of fear and parental devotion, the origin of injury-simulation. Two forms of this theory require consideration:—

(1) That in the instances of injury-simulation we see to-day, the bird is rendered temporarily incapable of co-ordinated movements by the clash of opposing impulses;

(2) That although in general the birds which we see simulating injury are following a stereotyped innate pattern and are not necessarily victims of hysteria resulting from thwarted impulses, these patterns arose through selection from ancestral cases of the first type, which happened to lure predators from the nest sufficiently often to give this unfortunate nervous derangement survival value and cause its evolution into a fixed habit.

In view of the facts just mentioned, I believe that both forms of this theory must stand or fall together. If it would suffice to suppose that some ancestral bird had such nervous instability that it fell into fits of uncontrollable panic whenever reproductive and self-preserved drives were brought sharply into conflict, although contemporary birds have outgrown this dangerous propensity, we might seriously entertain the theory. But if we accept the probable view that injury-simulation has arisen repeatedly, and will continue to develop in birds which adopt nesting habits that give such displays survival value, then form (2) of the theory becomes untenable. The reason for this is that the distribution of distraction displays makes it necessary to postulate some persisting innate foundation for them, not only in families in which they actually occur, but in others from which they are at present absent; for with changing modes of nesting these displays may acquire value, and then they will be likely to arise. In short, if unco-ordinated movements resulting from opposing drives are a necessary starting point for the evolution of distraction displays, then, given the probably recent origin of such displays in some species and the likelihood that they are still developing in others, the theory makes it necessary to suppose that many birds to-day exhibit panicky, uncontrollable movements when driven from their nests.

The general impression left by seeing many instances of injury-simulation by a great variety of birds in diverse circumstances, and by reading about many additional cases, is that the birds are in full command of their faculties and movements. I have never seen a single instance when it appeared otherwise; and the negative instances reinforce the conclusion drawn from the positive instances. If the conflict between fear and reproductive emotions led to unco-ordinated movements, we should expect the display to be conditioned solely by the strength of parental devotion—which bears no relation to the character or position of the nest—the nature of the potential enemy, and perhaps also the suddenness of its appearance. We should expect parents so devoted as kingfishers, emerging from their burrows in the river bank, to fall fluttering into the water; woodpeckers to drop from their holes in the tops of dead trees and creep over the ground, unable to fly; birds that nest amid dense vegetation to crawl and beat their expanded wings, becoming hopelessly entangled in the vines and bushes and an easy prey to their enemies; colonial ground-nesting birds to go staggering over the nests of their neighbours, causing great confusion and loss of eggs. Yet we see no such futile or disastrous exhibitions of uncontrolled movements; the tendency to fall into such fits would soon be eliminated by selection. On the contrary, we find that with few exceptions birds simulate injury only when the character and position of their nests are such that there is at least a good possibility that the ruse will serve a useful end.

Further, we should expect the panicky or temporarily crippled bird to fall an easy prey to its pursuer. But what man or dog has been fleet enough to

catch the bird that appears so helplessly injured as it flutters from its nest? We should not expect a panic-stricken bird to delay the manifestation of its symptoms until it had placed itself in a position peculiarly favourable for the display of its wild, unco-ordinated movements, nor to interrupt these vain flutterings when it reached the end of the favourable area, fly in a normal manner to another appropriate stage, then resume the display. We should not expect to see a parent bird, overcome by fear, attempt to defend its nest and then, finding its means of defence inadequate, suddenly change its tactics and try to decoy the intruder away. Still less should we expect to see the bird advance to meet the enemy before losing complete control over its movements, as Killdeers do; nor to see it deliberately place itself in a most perilous situation, as the Black-striped Sparrow which saved its fledgling from a dog.

I think, then, we must conclude that in nearly every case the injury-simulating bird is in full possession of its wits and control over its limbs, so much so that in many instances it performs movements which require a greater degree of controlled effort than its usual modes of locomotion, if only because they are less habitual; as swimming with most men calls for a greater concentration of the faculties than walking. The bird at times varies its tactics in a way that seems hardly possible without a grasp of the total situation and some understanding of the end to be achieved.

A further objection to the theory that injury-simulation grew out of the conflict between fear and parental solicitude is that it makes unwarranted assumptions as to the degree of terror a bird experiences. It is no more necessary to suppose that an animal is trembling with fear every time it retreats from an enemy than that a man is terrified whenever he scuttles out of the way of an automobile coming down the street. How little foundation we have for attributing blind terror or overpowering fear to the injury-simulating bird is brought out clearly by the experiences of Grimes (1936) with certain wood warblers in Florida. A Swainson's Warbler would not leave her eggs until *pushed* off, and even then she returned and tried to resume incubation by straddling the fingers that Grimes held over her nest. Yet when finally driven from her eggs she fluttered over the ground like a crippled bird, only to return in a few minutes and accept deer-flies from her visitor. A Prairie Warbler continued to feed her nestlings while he set up a camera a few feet from her nest, yet grovelled on the sand at his feet in what appeared to be a delirious fit of anxiety for her young when a movement of the photographer caused them to burst from the overcrowded nest. But after displaying so for a few seconds she calmly went about feeding her fledglings in their new surroundings. Likewise, it is hardly probable that the Kentish Plover was terrified by the Oyster-catcher before which he simulated injury, as Selous saw on the Dutch polders. My surmise is that the bird which gives a distraction display when its eggs or young appear to be in peril is far less anguished,

far less torn between the conflicting emotions of fear and parental devotion, than the parent bird who has no resource save to flit helplessly about and watch a more powerful animal approach its treasures. The displaying parent occupies itself with an elaborate act instead of passively awaiting the outcome of the enemy's advance. With us, at least, action assuages fear, and hope lingers on until the last resource has failed.

We said that the known distribution of distraction displays among the families and genera of birds makes it necessary to discover among contemporary birds some widespread, innate foundation upon which these displays can be built by a relatively slight and easily acquired genetic modification. The supposed tendency to fall into semi-paralytic fits when the instinct of self-preservation is suddenly thrown into conflict with reproductive urges fails to meet this requirement, for we have scarcely any observations which prove the occurrence of such incapacitating fits. Moreover, that a useful mode of behaviour should grow out of the weakness and inadequacy of an animal is inherently improbable. It is far more promising to seek the origin of such behaviour among its abilities than among its disabilities. We might, for example, look with advantage for the required widespread foundation of injury-simulation in intelligence, of which birds are not wholly devoid. In an animal whose subjective processes we cannot follow, our criterion for the presence of intelligence must be the ability to combine movements or activities in new ways, relevant to the actual situations of its life, as a result of individual experience. We call an animal intelligent when it can modify its behaviour to its own advantage, in a manner not strictly dictated by inheritance.

A discussion of the origin of distraction displays must take into account the great irregularity of their occurrence even among birds of the same species in the same locality, and the large measure of discrimination or judgment that enters into their use. The birds of a single population show far greater uniformity in such matters as the shape and position of the nest, the pattern of incubation, and the character of their songs, than in the employment of distraction displays, since some rather consistently use them while neighbouring members of the same species appear never to do so. To what degree this variability in the performance of distraction displays reflects individual experience and to what degree genetic factors are concerned, we lack all positive information. Although the complexity of the more elaborate distraction displays and their constancy of form in a species, or even in a genus, indicate an innate pattern, the successful use of injury-simulation demands a high degree of discrimination, lest it lead the parent bird into situations which will cost its life and, indirectly, that of its offspring deprived of adequate care. Scarcely anything a bird does is fraught with greater peril or requires a finer calculation of risks. One who has witnessed these displays in many birds in many circumstances can scarcely doubt that in employing them the birds use intelligence or something very like it.

When one considers the wide range of the learning abilities of birds as discussed by Thorpe (1951) and others, it hardly seems beyond their capacity to learn by experience that they can lure predatory animals from eggs or young by a slow and conspicuous retreat in front of the intruder. In all essentials save that of danger this feat is not greatly different from that of leading fledglings to safety by moving in front of them, with or without an enticing morsel in their bill. I have watched several kinds of finches lead to cover young just out of the nest by running slowly ahead of them with mincing gait, wings and tail drooping. Had they behaved in this fashion when a man or a quadruped visited their nest one would have called it a distraction display. The fledglings were in exposed positions, hence the actions of the parents who crept over the ground ahead of them were associated with danger to the young, although in one instance, when I was watching from a hide, no peril was in sight. Considering the emotional equivalence of the two situations, I believe that it is not beyond the capacity of many birds to employ for the purpose of luring an enemy from the nest the movements used in leading young to safety.

The view that distraction displays originate as intelligent or individually acquired behaviour would place them in the category of "secondary instincts", in the sense that this phrase was used long ago by Romanes. Although not without recent supporters, especially as applied to insects, this theory has fallen into disrepute because, in its original form at least, it implied the inheritance of acquired characters, for which there is a dearth of convincing evidence. But if we combine the concept of secondary instincts with that of organic selection (MacDougall 1918; Huxley 1948 for earlier references) it need not smack of biological heresy. The theory of organic selection assigns to mind or intelligence its due share in influencing the course of evolution, not only in man but in all the more intelligent animals. Hence it makes it easier for us to understand the evolution of intelligence itself; for if intelligence has had no influence upon the course of evolution in the animal world, it can hardly have been produced by the generally understood methods of evolution. The first step in organic selection, which might also be called "mental selection", is the appearance of what I term a "precursory habit", an individually acquired mode of conduct which prepares the way for heritable modifications in structure, and correlated patterns of behaviour, that will finally incorporate these habits into the innate endowment of the animal's descendants. Only the subsequent history of a line of animals will tell whether any observed habit, supposed to be individually acquired, is in fact the precursor of an important genetic modification.

Because it is easier to visualize the mode of operation of organic selection when the precursory habit brings about a conspicuous modification in gross structure than when it merely leads to its own perpetuation as an innate mode of behaviour, to make the concept clearer let us consider, before passing on to

the problem which particularly concerns us here, a hypothetical case of the former sort. Sometimes I have seen a Neotropical House Wren climbing over the bark of a tree to pluck small invertebrates from the crevices, in the manner of a tree-creeper or a woodhewer. This habit is rare enough in the species to appear to be individually acquired rather than innate; it seems that some of the wrens learn by direct observation that this is a profitable way to hunt. Let us suppose that such bark-inspection becomes more common in a population of wrens, possibly as a result of imitation. Then, if in their district the bark of trees provides a rich, scarcely exploited supply of food, any mutations that cause such modifications in the structure of feet, bill, tail, or muscles of these wrens that they become more capable creepers will at once have survival value and tend to be preserved. Innate modes of behaviour will doubtless keep pace with structural improvements and ensure their efficient use. Thus, with the passage of the centuries, the individually acquired habit of hunting over tree-trunks will have been the precursor of a new genus or possibly a new family of birds, highly specialized for this mode of foraging, like the tree-creepers. As Huxley remarked, the process of organic selection simulates Lamarckian evolution, but actually consists in the replacement of acquired modifications by mutations.

In the foregoing pages we gave examples of all degrees of display by birds driven from their nests, from simple wing-quivering to the most convincing imitation of the actions of a disabled bird. I hold it probable that the latter gradually evolved from the former, and that contemporary birds exhibit all stages in the development of that remarkable habit commonly called "injury-feigning". It is certainly not unlikely that a bird whose parental devotion causes it to leave its threatened nest slowly and reluctantly, perhaps hopping over the ground with quivering wings, may draw the predatory animal in pursuit without foreseeing this result, that it saves its eggs or young by thus diverting the intruder, and that it learns by this experience to repeat the slow departure when its nest is again similarly menaced. From such a starting point we might suppose some elaboration of the slow and conspicuous departure from the nest by individual birds, as a result of their personal experience; but I hold it probable that a high degree of elaboration, such as we find in the most realistic examples of injury-simulation, would have to be assisted by genetic changes.

Intelligence, as we know, has an innate foundation, so that some neighbouring individuals will probable be equally endowed, and their capacity will be transmitted to their descendants. Since minds similarly constituted tend to respond to the same situation in the same way, we may suppose a population of birds in which a significant number of individuals learn to lure predators from their eggs or young, and that they make use of this knowledge often enough to give them better success in nesting than their less observant neighbours. In such a population any slight mutation which increased the

effectiveness of the distraction display and tended to make it a heritable character would immediately have survival value. Without this matrix already prepared for its reception, the mutation might lack present importance and be lost.

In his excellent discussion of diversionary display, Armstrong (1949) pointed out how, by incorporating into the birds' movements of retreat from a threatened nest elements taken from other contexts, the effectiveness of the distraction display is increased. Thus, when luring enemies from their nests, some birds simulate chicks begging for food, others make use of courtship movements or those employed as threats to rivals. Probably only a slight genetic change would be needed to transfer such innate patterns from their original context to that of slow retreat from the nest in the presence of an intruder. Although in his earlier discussion Armstrong (1942) closely associated "injury-feigning" with "trance states", his latest and most mature published views on the subject of diversionary display fit in well with those we have been developing.

Another advantage of a theory which postulates only slight genetic changes in the origination of distraction displays is that it can more readily account for their loss when environmental changes or altered nesting habits render them no longer useful, as must frequently have happened in the long history of birds. If the mutation of a single gene, or even changes in the positions of genes, can give rise to a structure or a function, a relatively slight mutation in the genotype might cause its disappearance.

Possibly a certain Grey-headed Tanager whose nest I often visited showed me injury-simulation in the process of evolution. Most tanagers build their nests well above the ground, and I have watched many members of the family without ever having seen one give a developed distraction display. This particular Grey-headed Tanager had placed her open cup only 53 inches above the ground in a coffee bush, not far from the high forest where she and her mate spent most of their time. So long as her nest held eggs, my approach would send her discreetly away while I was still at a distance. But on the day her nestlings hatched she sat bravely until I was scarcely two yards from her, then dropped to the ground and hopped slowly and at times haltingly away, as though her legs were stiff. But she did not flutter her wings nor beat them on the ground, and as an actor in the role of an injured bird she was hardly convincing. Yet perhaps this low-nesting tanager of the tropical forest and its neighbourhood is on the road to the development of a finished performance of injury-simulation which bird-watchers of a future generation will witness.

SUMMARY.

1. Some birds steal unobtrusively from the nest while a man is a long way off, others wait until he is almost within arm's length. The same individual may abruptly shift from one of these procedures to the other; or one member of a pair may follow the

first method and the other the second. Both of these modes of departure are strategically sound; but any intermediate course needlessly exposes the nest to detection.

2. If a bird delays with its eggs or young until an enemy has come very close it has one last resource: it may try to lure the intruder away by a distraction display, or "feigning injury".

3. Typical injury-simulation is merely a highly developed form of conspicuous departure from the nest, of which many examples are given. Such departure, which does not suggest disablement, may be either over the ground or by a peculiar slow flight.

4. Injury-simulation may begin after an unsuccessful attempt to defend the nest. Birds are careful to select unobstructed ground for this display, which may be interrupted while they pass over tangled vegetation and resumed in a clear area on the farther side. Endless variations in the mode of giving distraction displays suggest great discrimination and the intelligent adaptation of an essentially innate pattern to fluctuating circumstances.

5. Injury-simulation is on the whole confined to species whose nests are so placed that it is likely to be effective, chiefly to those whose open nests are on or near the ground. It is rare in birds whose eggs are placed high in trees, in holes, in elaborate closed nests, or in crowded colonies.

6. There are many records of the effectiveness of distraction displays with men and other mammals. But a Sclater's Antbird *Myrmeciza exsul* tried unsuccessfully to lure an Agouti *Dasyprocta* from its nest.

7. Of other parental stratagems, "freezing" in an upright posture on the nest's rim has been observed only in the Cedar Waxwing *Bombycilla cedrorum*. Nest-building to distract attention from a near-by occupied nest, and stuffing with fresh material the door of an occupied nest, have been reported for certain wrens. Eggs are seldom covered over during the parents' absence, although the expedient would seem to afford some protection. As fledglings fly weakly from the nest, the adults of some species fly close above them in "shielding flight", which may give a measure of security from aerial predators.

8. Distraction displays appear to be acquired with relative ease by species whose mode of nesting makes them effective, and are perhaps almost as easily lost when changed nesting habits render them useless. Hence it is necessary to postulate an innate foundation, widespread in birds, upon which these displays can be built with readily acquired genetic modifications. It is suggested that this foundation is the bird's intelligence or ability to learn by experience the effectiveness of this ruse. In a race of birds in which individually acquired distraction displays are somewhat frequent, genetic mutations tending to reinforce or elaborate such behaviour, at the same time making it heritable, would at once have "survival value", which otherwise they might lack. It is probable, then, that distraction displays have often been built up by "organic selection", or the gradual replacement of individually acquired traits by genetically transmitted characters.

REFERENCES.

- ALLEN, F. H. 1936. Auk 53: 125-127.
 ARMSTRONG, E. A. 1942. Bird Display. Cambridge.
 ARMSTRONG, E. A. 1947. Bird Display and Behaviour. London.
 ARMSTRONG, E. A. 1949. Diversionary display. Ibis 91: 88-97, 179-188.
 BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Nat. Mus., Bull. 179.
 CHERRIE, G. K. 1916. A contribution to the ornithology of the Orinoco region. Mus. Brooklyn Inst. Arts Sci., Sci. Bull. 2: 133a-374.

- CHISHOLM, A. H. 1936. Injury feigning in birds. *Auk* 53: 251-253.
 DANFORTH, R. E. 1930. The Sparrow-hawk's first flight. *Sci. Mon.* 30: 81-84.
 FRIEDMANN, H. 1934. The instinctive emotional life of birds. *Psychoanal. Rev.* 21 (3) and (4). (Sep. pag. 1-57.)
 GREY OF FALLODON 1927. *The Charm of Birds*. New York.
 GRIMES, S. A. 1936. "Injury feigning" by birds. *Auk* 53: 478-480.
 HERRICK, F. H. 1905. *The Home Life of Wild Birds*. New York.
 HOWARD, L. 1952. *Birds as Individuals*. London.
 HUXLEY, J. 1948. *Evolution, the modern Synthesis*, 5 imp. London.
 HUXLEY, J. S. & MONTAGUE, F. A. 1925. Studies on the courtship and sexual life of birds. V. The Oyster-catcher (*Haematopus ostralegus* L.). *Ibis* (12) 1: 868-897.
 MACDOUGALL, W. 1918. *Body and Mind*, 5 ed. London.
 MILLER, A. H. 1951. The "rodent-run" of the Green-tailed Towhee. *Ibis* 93: 307-308.
 MILLER, J. R. & MILLER, J. T. 1948. Nesting of the Spotted Sandpiper at Detroit, Michigan. *Auk* 65: 558-567.
 MOREAU, R. E. & MOREAU, W. M. 1937. Biological and other notes on some East African birds. *Ibis* (14) 1: 321-345.
 MOUSLEY, H. 1939. Nesting behavior of Wilson's Snipe and Spotted Sandpiper. *Auk* 56: 129-133.
 NICE, M. M. 1939. *The Watcher at the Nest*. New York.
 NICE, M. M. 1943. Studies in the life history of the Song Sparrow, II. *Trans. Linn. Soc. N.Y.* 6: 1-328.
 NICE, M. M. & THOMAS, R. H. 1948. A nesting of the Carolina Wren. *Wilson Bull.* 60: 139-158.
 ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee. *Auk* 58: 518-535.
 RUSSELL, H. N., Jr. & WOODBERRY, A. M. 1941. Nesting of the Gray Flycatcher. *Auk* 58: 28-37.
 SELOUS, E. 1927. *Realities of Bird Life*. London.
 SKUTCH, A. F. 1940. Social and sleeping habits of Central American wrens. *Auk* 57: 293-312.
 SWARTH, H. S. 1935. Injury-feigning in nesting birds. *Auk* 52: 352-354.
 TAVERNER, P. A. 1936. Injury feigning by birds. *Auk* 53: 366.
 THORPE, W. H. 1951. The learning abilities of birds. *Ibis* 93: 1-52, 252-296.
 WILLIAMSON, K. 1952. Regional variation in the distraction displays of the Oyster-catcher. *Ibis* 94: 85-96.

APPENDIX: SCIENTIFIC NAMES OF BIRDS.

Antbird, Bicoloured—*Gymnophis bicolor*
 Antbird, Scater's—*Myrmeciza exsul*
 Antbird, Tyrannine—*Cercomacra tyrannina*
 Antshrike, Bridges'—*Thamnophilus bridgesi*
 Antshrike, Spotted—*Thamnophilus punctatus*
 Antvireo, Olivaceous—*Dysithamnus mentalis*
 Antwren, Slaty—*Myrmotherula schisticolor*
 Becard, White-winged—*Pachyrhamphus polychropterus*
 Brush-finch, Striped—*Atlappetes torquatus*
 Bunting, Yellow—*Emberiza citrinella*
 Cacique, Yellow-rumped—*Cacicus ccla*

Catbird—*Dumetella carolinensis*
 Chickadee, Black-capped—*Parus atricapillus*
 Chlorophonia, Turquoise-naped—*Chlorophonia occipitalis*
 Cowbird, Giant—*Psomocolax oryzivorus*
 Cuckoo, Rufous-rumped—*Morococcyx erythropygus*
 Cuckoo, Yellow-billed—*Coccyzus americanus*
 Dendrocincla, Northern—*Dendrocincla anabatina*
 Dipper, White-backed—*Cinclus leucocephalus*
 Dove, Cassin's—*Leptotila cassini*
 Dove, Ground—*Columbigallina passerina*
 Dove, White-fronted—*Leptotila verreauxi*
 Duck, Mallard—*Anas platyrhynchos*
 Flycatcher, Grey—*Empidonax griseus*
 Gnatcatcher, White-browed—*Poliotila plumbea*
 Hawk, Sparrow—*Falco sparverius*
 Hummingbird, Barrot's Fairy—*Heliothrix barroti*
 Jay, White-tipped Brown—*Psilorhinus mexicanus*
 Killdeer—*Charadrius vociferus*
 Kingbird, Neotropical—*Tyrannus melancholicus*
 Kiskadee—*Pitangus sulphuratus*
 Kite, Swallow-tailed—*Elanoides forficatus*
 Lark, Horned—*Otocoris alpestris*
 Manakin, Blue-capped—*Pipra coronata*
 Manakin, Salvin's—*Manacus auranriacus*
 Manakin, Yellow-collared—*Manacus vitellinus*
 Oropéndola, Montezuma—*Gymnostinops montezuma*
 Owl, Great Horned—*Bubo virginianus*
 Owl, Long-eared—*Asio otus*
 Owl, Short-eared—*Asio flammeus*
 Oyster-catcher—*Haematopus ostralegus*
 Partridge—*Perdix perdix*
 Pauraque—*Nyctidromus albigollis*
 Pigeon, Red-billed—*Columba flavirostris*
 Pipromorpha, Oleaginous—*Pipromorpha oleaginea*
 Plover, Kentish—*Charadrius alexandrinus*
 Plover, Kittlitz's Sand—*Charadrius pecuarius*
 Plover, Semipalmated—*Charadrius hiaticula*
 Quail, Bob-white—*Colinus virginianus*
 Redstart, American—*Setophaga ruticilla*
 Redstart, Collared—*Myioborus torquatus*
 Redstart, Slate-throated—*Myioborus miniatus*
 Sandpiper, Spotted—*Actitis macularia*
 Seed-snip, Patagonian—*Thinocorus rumicivorus*
 Snipe, Wilson's—*Capella gallinago*
 Sparrow, Black-striped—*Arremonops conirostris*
 Sparrow, Orange-billed—*Arremon auranrirostris*
 Sparrow, Song—*Melospiza melodia*
 Sparrow, Yellow-thighed—*Pseliophorus tibialis*
 Stilt, New Zealand Pied—*Himantopus himantopus*
 Swallow, Rough-winged—*Stelgidopteryx ruficollis*
 Tanager, Grey-headed—*Eucometis penicillata*

- Tanager, Song—*Ramphocelus passerinii*
Tit, Great—*Parus major*
Tityra, Band-tailed—*Tityra semifasciata*
Tityra, Inquisitive—*Tityra inquisitor*
Toucan, Swainson's—*Ramphastos swainsonii*
Towhee, Green-tailed—*Chlorura chlorura*
Towhee, Red-eyed—*Pipilo erythrophthalmus*
Trogon, Mexican—*Trogon mexicanus*
Warbler, Black-throated Green—*Dendroica virens*
Warbler, Buff-rumped—*Basileuterus fulvicauda*
Warbler, Chestnut-sided—*Dendroica pensylvanica*
Warbler, Hooded—*Wilsonia citrina*
Warbler, Kentucky—*Oporornis formosus*
Warbler, Parula—*Parula americana*
Warbler, Pine—*Dendroica pinus*
Warbler, Prairie—*Dendroica discolor*
Warbler, Swainson's—*Limnothlypis swainsonii*
Warbler, Yellow—*Dendroica petechia*
Warbler, Yellow-throated—*Dendroica dominica*
Waxwing, Cedar—*Bombycilla cedrorum*
Whip-poor-will—*Caprimulgus vociferus*
Woodpecker, Golden-fronted—*Centurus aurifrons*
Wren, Bay—*Thryothorus nigricapillus*
Wren, Carolina—*Thryothorus ludovicianus*
Wren, Neotropical House—*Troglodytes musculus*
Wren, Spotted-throated—*Thryothorus rutilus*
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