THE PARENTAL STRATAGEMS OF BIRDS.

By ALEXANDER F. SKUTCH.

Received on 8 January 1954.

I. THE NESTING BIRD'S ALTERNATIVES : CLOSE SITTING OR INCONSPICUOUS DEPARTURE.

No matter how carefully a bird hides away her nest, nor how completely she blends with the surroundings as she sits in it, at the moment of departure she becomes conspicuous as a moving object, and is in danger of revealing her secret. Every bird-watcher has had his attention drawn, by the bird's sudden departure, to many a nest that might otherwise have escaped detection. The act of leaving the nest is almost as likely to betray its position as the approach to it. Birds are aware that they risk disclosing the location of the nest at the moment of flying away, and time their departure accordingly. Those that nest in holes come to the entrance and look carefully around before darting out. If they espy predatory creatures of certain kinds, especially those which menace their eggs or nestlings rather than themselves, they may draw back inside to await a more propitious moment for taking flight. In the Guatemalan highlands I devoted much time to watching the nest of a pair of brilliant Mexican Trogons*, situated in a low, decaying stub at the edge of an oak wood. One day, as the male trogon was about to fly from the cavity in response to the call of his mate, who had come to replace him in brooding the nestlings, he noticed a squirrel moving about among the bushes about 20 feet away. Although already halfway through the doorway, he cautiously backed into the chamber and waited there until the rodent had departed. To have flown forth in the animal's presence might well have cost the lives of the nestlings.

Birds when undisturbed leave their nests as quietly and inconspicuously as possible, as one may see while watching them from concealment. When a potential enemy approaches, the sitting bird may do one of two things: it may steal away while the intruder is still a good distance off, trying to avoid being seen; or it may sit motionless, hoping by its immobility to escape detection. Some birds are so alert and shy that it is almost impossible to glimpse them as they incubate or brood; often I have been unable to learn to what bird a nest belonged until I concealed myself near by and awaited the owner's return. Other birds, as is well known, will sit motionless until one is almost upon them, sometimes even allowing themselves to be touched by the human hand. Birds which nest in cavities in trees will

* Scientific names of species mentioned in the text are all given in an appendix.

frequently tolerate much shaking and pounding on the trunk before they come to the entrance and reveal themselves. Each is trying in its own way to avoid detection; for their eggs and young are coveted by a host of enemies of the most diverse sorts. Just how any nesting bird will act in the presence of a hostile creature depends upon many circumstances: the nature of the predators in the region; whether it has been much or little persecuted by man; the local experience of its kind and its own individual experience; whether or not its eggs are on the point of hatching; the situation of the nest, whether high or low. But as a rule brightly coloured birds attempt to steal away before the potential enemy has come near enough to see them; inconspicuously clad birds sit closely, for their chances of escaping detection are good if only they remain perfectly immobile on the nest.

Flight so prompt and unobtrusive that it fails to catch the approaching eyes; motionless sitting until the last moment consistent with personal security—these are the bird's only strategically sound modes of procedure when a hostile animal more powerful than itself advances toward the nest. To remain sitting until the creature has approached near enough to enjoy an unobstructed view, yet to fly while there is still a doubt that it has noticed the nest, is vacillating behaviour that needlessly exposes the eggs or nestlings to detection and destruction. In lowland tropical forest, where eight or nine nests in every ten are pillaged before the young are fledged, few birds can afford to behave in this dangerous, undecided fashion. Of the kinds that nest among the undergrowth, some steal away so promptly upon a man's approach that only with the utmost caution can he come near enough to enjoy a glimpse of them; others in the same habitat will suffer him to advance within arm's length, or even to touch them.

I once found a nest of the Slaty Antwren, a small, inconspicuous denizen of the heavy forest in southern Costa Rica, that hangs its frail open nest a yard or two above the ground. The female when incubating would allow me to advance within a foot of her, then drop to the ground and struggle away as though injured; but the male antwren, no brighter in plumage than herself, always departed the nest so soon and so stealthily that, until I concealed myself in a blind, I never enjoyed a good view of him as he sat. At a second nest of the same species the situation was exactly the reverse: the female would make off as soon as she glimpsed me; the male would sit until I stood over him, then jump from the nest and attempt to lure me away. It is inconceivable that my distance from them when they took flight was a measure of their fear or confidence in my presence. Why should the female of one nest and the male of the other be so fearless, their respective mates so shy? I am certain that none of the four was terror-stricken by my approach; they merely acted with due caution, and had chosen one or the other of the two methods which best safeguarded their persons and their nests.

Thirteen years later, in the forest near my house in the valley of El General in Costa Rica, I found a nest of the Slaty Antwren where the parents behaved somewhat differently. When visiting this nest I came suddenly into view of it on emerging from a dense tangle of vines at a spot about 60 feet away from it; but from this point I advanced through forest with little undergrowth, in sight of the nest the whole way. Unlike the earlier pairs, the male and female behaved in much the same way : both either slipped from the nest the moment I passed out of the tangle of vines, and so rapidly that I scarcely caught a glimpse of them, or both remained sitting while they watched me approach over a distance of about 50 feet, then, when I had reached a point two or three yards from them, jumped from the nest and gave a fine distraction display. But they never left while I was in the middle of the course over which they could watch me approach. The transition from prompt flight to close sitting was quite sudden. The set of two eggs was completed on 21 May, but until 29 May I was never given a good view of the sitting parent, which fled the moment it espied me. On this date the male allowed me to come close, then simulated injury. On 31 May the female for the first time permitted a near approach, then displayed. But on 3 June, whichever parent was sitting slipped away before I could identify it. Thereafter, until the week-old nestlings were killed by a predator on 12 June, both parents would sit until I came quite near, then give a fine distraction display. The behaviour of these two antwrens was, throughout the period I had them under observation, perfectly consistent. They always chose either one or the other of the only modes of departure compatible with the welfare of their nest : immediate flight or delay until there could be no doubt that I had seen them, with a preference for the second alternative as parental devotion increased. I do not know whether they had deliberately thought out their problem, but if they had asked for my advice I could not have suggested any improvement on their strategy.

At yet another nest of this antwren, throughout the incubation period both parents rather consistently fled away at my approach, so that I rarely even glimpsed them. On the single occasion when I actually saw a parent sitting it was the female, who allowed me to come fairly close, then dropped almost to the ground and flew away.

A female Yellow-collared Manakin, who had built her tiny cupped nest beside a forest trail in Panamá, was at first so shy that she never allowed me a glimpse of her little olive-green figure as she sat in it, and only the warmth of her two eggs told me that she had just forsaken them. But one day she amazed me by continuing calmly to incubate while I came up to her, bent over, and almost touched her with my finger-tips. It is hardly likely that her character changed from timorous to bold in a single day. But with growing devotion to her nest she had changed her tactics; and between immediate flight and departure at the last moment there was no mode of procedure

consistent with that devotion. Birds which build their nests where they are accustomed to see men moving about them may, if they have not been persecuted, sit quietly while people pass very close, but fly away if one stops to look at them with intention. Birds of the lowland forests of tropical America are less confiding, and their conduct seems strangely inconsistent unless one remembers that there are only two prudent modes of behaviour, and all intermediate courses are folly, at least when the intruder is a flightless animal.

I have sometimes wondered how often I have passed within arm's length of a nest for which I was assiduously searching, failing to discover it while the owner sat motionless, watching me. We have no way of knowing from how many of her non-human enemies a bird saves her nest by the same tactics; but probably the number of them is high.

When a bird lingers on the nest in an attempt to escape detection, only to be discovered by her more powerful enemy when dangerously near, she has one last resource at her command. She may try to draw the animal's attention from her nest, which is immobile and entirely at his mercy, to herself, who has wings to escape him. So instead of stealing unobtrusively away, as birds almost invariably do when there is still hope of avoiding detection, she makes herself more than ordinarily conspicuous, moving with deliberate slowness, as if to tempt the animal onward with the prospect of an easily captured meal. Often she goes fluttering or creeping over the ground, as though a wing or a leg were broken, leaving her incapable of flight or of rapid walking.

Such behaviour by nesting birds occurs among the most diverse families and in all parts of the world, and has long been known. It has been given the most varied names : " feigning injury ", " feigning a broken wing ", " the broken-wing ruse ", " the parental ruse " (Selous 1927), " disablement reaction " (Armstrong 1942), " lure display " (Williamson 1952), etc. Technically by far the best term for the phenonemon as a whole is " distraction display " (Nice 1943), for such behaviour serves to distract the attention of a potential enemy from the nest or young to the parent; and we can use this designation without prematurely committing ourselves on the debatable point of whether the bird is or is not consciously simulating injury. Unfortunately, like so many good technical terms, it is not so picturesquely descriptive as some of the earlier designations. More recently Armstrong (1949) has proposed an elaborate classification and nomenclature for the varied types of behaviour, all of possible service in deflecting intruders from the nest, which he subsumes under the general heading " diversionary display ". He prefers " injury-simulation " to " injury-feigning ", because it does not so obviously attribute deliberate deceit to a bird.

The explanations of this behaviour, so surprising to one who witnesses it for the first time, are various and conflicting. W. H. Hudson, usually so discerning an observer, supposed the parent bird to be in pain, and temporarily

incapable of flight. Others have thought that it " becomes deliriously excited and has a fit ". Friedmann (1934) supposed such injury-feigning to be caused by muscular inhibition; the conflict between fear, urging the bird to make off with all haste, and parental devotion holding it to the nest, results in a crippled departure. Thus the observed behaviour is " a compromise between fear and reproductive emotions ", and the conduct of the bird is " hysterical ". The view of Armstrong (1942, 1947) was only slightly different; he associated injury-feigning with going into a trance or " playing 'possum " in the face of danger—a phenomenon far more rarely witnessed among birds. He believed that it might be " a halfway house on the road to a trance condition ", and that it results from " a greater or lesser degree of disorganisation in the behaviour-patterns ". Other writers, on the contrary, believe that the performers act with a purpose and " appreciate what they are doing " (Chisholm 1936).

It will be well to keep these two conflicting views in mind while reading the accounts of injury-simulation which follow. If the bird is in fact undergoing a fit, or suffering from some temporary muscular impediment, or hysterical, or on the verge of falling into a trance, we should expect its movements to be more or less unco-ordinated and uncontrolled; we should expect that it would frequently strike against obstructions, become entangled in the vegetation, or fall an easy prey to its pursuer. If it is in full control of its faculties and acts with a purpose, whether definitely visualized or not, we should look for it to make none of these blunders but, at least in most cases, successfully to elude its enemies and confuse them as to the true position of its offspring.

2. CONSPICUOUS DEPARTURE FROM THE NEST.

In order to reach just conclusions we should consider a phenomenon not in isolation, but as one of a class or group of kindred manifestations. Until fairly recently it was the custom to look upon injury-simulation as an isolated phenomenon in the behaviour of birds, rather than to consider it in relation to kindred actions. It seems that we even lack a designation which embraces the whole class of actions to which I would refer. Edmund Selous used, apparently in a more restricted sense, the term " parental ruse ", which is broader than " distraction display " and sufficiently general to cover all the behaviour I have in mind; but unfortunately the plural is not euphonious. Largely on grounds of euphony I prefer the phrase " parental stratagems ". If we consider injury-feigning not as a phenomenon standing in isolation but merely as the most common and familiar of the expedients which parent birds employ to save their eggs and young from enemies more powerful than themselves, I believe we shall be in a position to reach a truer conception of its nature and significance; and perhaps we may even find some indications of its mode of origin.

Simulating injury, as many birds do it, is a complex display. Either the bird that behaves in this fashion is in fact so frightened or distressed as to be incapable of co-ordinated movements, or it is a consummate actor. Assuming for the moment that the bird is " putting on " with a definite purpose, it seems probable that such a convincing and highly finished show was not made ready for the audience without a good deal of rehearsing—ancestral rehearsing, by actors who became dust before the dawn of human history. While this is true of the companies of actors that now produce a faultless show—the species with perfected injury-simulation—is it not possible that still other troupes are rehearsing at the present moment, and will present an equally accomplished act to our posterity?

Injury-simulation is merely one of the perfected forms of conspicuous departure from the nest—departure which serves to draw the attention of an intruder from the nest and its occupants to the withdrawing bird. At times we do in fact witness birds leaving their nests, in the presence of a potential enemy, in a manner which appears to be deliberately calculated to attract attention, yet which certainly does not create the impression that the departing bird is crippled. Such departure may be injury-simulation in process of development, it may be vestigial injury-simulation, or it may be that the act has merely been abbreviated or suppressed from one cause or another. But at all events, such displays are suggestive; they yield a clue as to how the perfected act might have arisen.

One May I found a Red-eyed Towhee building her nest among the dead leaves at the foot of a low blackberry bush in open oak woods in Maryland. When the bulky cup had been completed and the female bird was incubating her three eggs, she would sit quietly until I almost touched her, then jump from the nest and hop slowly away over the dead leaves, as though to attract attention. At length, having gained sufficient distance, she would fly up to a low branch and call " tow-he ". She did not wildly beat her wings, nor fall over on her side, nor in any other way suggest that she was not in full possession of her faculties. Only the unusual slowness of her progress attracted attention. When watched from concealment, each time she left her eggs to hunt for food she took a single hop from the nest and winged away. This towhee's mode of departure from her nest when alarmed was far less specialized than the " rodent-run " of the Green-tailed Towhee described by Miller (1951), but the latter might have evolved from simple behaviour like that of the Red-eyed Towhee.

A somewhat more spectacular mode of departure was adopted by a Kentucky Warbler nesting not far from the towhee. She would sit, brooding her nestling in the cup of dead leaves among sanicle in the moist woodland, while I bent over with my head hardly more than a foot from hers; but when I made a move to touch her she jumped abruptly from the nest and walked slowly over the ground with the tips of her wings dragging, chirping excitedly.

Her departure suggested reluctance and a desire to attract attention, but no lack of muscular co-ordination—no true injury-simulation. Another of her kind, whose feathered nestlings, when I came within two inches of treading upon the unseen nest, scuttled away with a loud explosion of small voices, crept about more slowly, dragging her relaxed wings and tail and appearing to be in agony.

As I walked through a scrubby pasture in the Cauca Valley of Colombia, a Ground Dove fluttered out from beneath a little Lantana bush and walked slowly, mincingly away, thereby advising me that he had a nest very close to where I stood. Looking about me, I promptly discovered it on the ground in the scant shade of the bush. While my notes written at the time mention an initial flutter, what I distinctly remember after the lapse of several years is the strikingly slow, deliberate, walking departure from the eggs. It certainly was not feigning injury, but it did attract attention.

The instances might be multiplied, but they are sufficient to show that a deliberately slow and conspicuous departure from the nest does not always convey the impression that the bird is injured or unable to co-ordinate its actions, even in species that do at times simulate injury. Such needlessly slow withdrawal from the nest is not confined to birds that build or lay their eggs upon the ground. One March I found a nest of a Blue-capped Manakin, a shallow hammock suspended by its rim between two spiny petioles of a small palm in the dim undergrowth of heavy forest. Hung only 38 inches above the ground, the nest was so small and neat that it was almost hidden beneath the tiny green bird as she sat. From the first she would permit a very close approach; as the two eggs neared the date of hatching she would linger until I was scarcely more than a yard away, then drop nearly to the ground and skim just above it with a peculiarly slow, fluttering flight, continuing so until lost to view amid the underwood. I almost expected that she would eventually come to the ground and drag herself over it, simulating injury, but she never did so. This type of distraction-display is unknown in the manakin family, although the female Blue-capped Manakin has a more stationary display which will be described below. A female Salvin's Manakin, whose scarcely higher and still slighter nest I found amid the undergrowth of the same Costa Rican forest, fled it with the same slow, fluttering, descending flight, but did not give quite so good a display as her smaller neighbour. Another Salvin's Manakin, nesting in an orange tree in a pasture, dropped to the grass and skimmed over it for about 20 feet, but went too fast to suggest that her strength was failing.

But the most arresting display of deliberately slow flight that I have ever witnessed was repeated many times for my benefit by a pair of tiny White-browed Gnatcatchers. Both sexes together had built the exquisite little downy cup, ten feet above the ground in a murta tree standing in a pasture and five or six yards from the vine-festooned trees that shaded the San Antonio

River in southern Costa Rica. Male and female took turns at warming the three speckled eggs. Although the male sat for longer periods and was less readily frightened from the eggs than his mate, she had the more engaging manner of taking leave when I disturbed her. Whenever I walked beneath the nest she would drop well below the supporting limb, then rise to the tops of the trees on the bank of the neighbouring river with a most peculiar, beautiful flight. Hanging beneath her rapidly vibrating wings, moving with extraordinary slowness, she seemed to float rather than fly from the nest. The upright position of her long tail supplied the necessary drag on her forward progress and made such slow flight possible. Until the morning when the nestlings were five days old the female gnatcatcher always rose up to the riverside trees upon being disturbed on the nest. But now, as she fled upon my arrival, she skimmed low over the pasture with tail erect in fluttering flight until, after covering about 50 feet, she came to rest in a low bush. When I approached she flew nearly as far again in the same fashion, maintaining a height of about a yard above the low grass. I continued to follow, but could not make her repeat her pretty display the third time. The male gnatcatcher, although more devoted to the nest than his mate, flew so in my presence only once. On the afternoon the eggs hatched he rose from the nest to the trees beside the river in this slow fashion, his tail held erect.

Such " butterfly flight ", to use a term applied by Huxley and Montague (1925) to one of the slow flights of the Oyster-catcher, seems the equivalent of injury-simulation by a ground-nesting bird. The gnatcatcher appears to fly with failing strength, scarcely able to make its way through the air. Actually, to fly so must require a good deal more skill and muscular co-ordination than to go in the habitual fashion. I saw the gnatcatchers' nest endangered only once. A small and very slender snake had climbed the rough bark of the trunk and was coiled on a dead twig close beside the tiny cup. The male gnatcatcher, far smaller than the snake, was darting within a few inches of the serpent's wide-open red mouth, making feints of attack and uttering almost continuously his fine nasal mews. On this occasion the bird did not call the slow flight into service—at least, not after his cries drew my attention, in time to save his eggs.

Other nest-robbers with which the gnatcatchers almost certainly have to contend are Swainson's Toucan and the Swallow-tailed Kite. I do not believe that the ruse could be of much avail where the great-billed clumsy toucan is concerned. But the kite subsists largely upon insects that it catches in its talons while soaring; and the slow-flying gnatcatcher resembles a big grasshopper rather than a bird. This is merely a hint; I have never seen a kite visit a gnatcatcher's nest, although it has in my presence pulled the nestlings of other birds from nests in similar positions. But could so tiny a winged creature as the gnatcatcher escape so superb a master of flight as the kite if once she lured him on ? Possibly, if she had already calculated the

distance to a neighbouring tree whose close-set branches would form a barrier to the wide-winged pursuer. The gnatcatcher's sudden and inconspicuous drop below the nest, before she begins to flutter conspicuously away, would help confuse the enemy as to its true position.

3. DISPLAY AFTER LEAVING THE NEST.

Other birds depart the threatened nest in a normal, inconspicuous fashion, and first begin their displays a short distance away, usually on the opposite side of the intruder. The little dull, olive-green flycatcher of tropical America called the Oleaginous Pipromorpha fashions one of the most marvellous nests in the whole kingdom of birds. It is attached to the dangling, cord-like root of an air-plant or a slender swinging vine, beside a river or in the undergrowth of the forest. The pear-shaped mass of green moss is penetrated on one side by a narrow, round doorway that leads to a chamber softly padded with fine fibres from the heart of a decaying palm-trunk. The female alone attends the two or three white eggs, for the males of her kind are off in the forest, singing a tuneless song and flitting their dull wings all through the nesting season, too busy by far proclaiming their presence to the other sex to attend any nest.

As a rule, when her nest is approached, the little green pipromorpha will dart out and vanish without ever allowing a satisfactory glimpse of herself. But sometimes, when the eggs are about to hatch, she will cling to them until the latest moment consistent with the duty of self-preservation, then dart to a neighbouring low perch and flick her wings alternately above her back with more than wonted energy, while she watches the intruding naturalist examine her treasures. I say " more than wonted energy ", because the habit of raising the wings momentarily above the back, one at a time, is a distinguishing mannerism of the pipromorpha. It is hardly possible to watch one of these flycatchers for a minute without observing this idiosyncracy, whether the bird feeds or rests or sings in a courtship gathering. But the wing-raising becomes more than ordinarily brisk and frequent when the mother-bird is watching a nest that appears to be in danger. Apparently the accelerated wing-flicking is a manifestation of excitement in itself of no significance; birds react to great nervous stress in the most unexpected manners, as when they sing while their nest is being plundered, or even when wounded.

A more developed display of this nature is sometimes given by another diminutive olive-green bird of the same forests, the female Blue-capped Manakin. After sitting on her nest until I almost touched her, she has fluttered down to some slender perch close to the ground, where she slowly fluttered her widely spread wings, often appearing to be precariously balanced and on the point of falling. A pretty little trill usually calls attention to this performance, and at times the manakin seems deliberately to wait until one's eyes are turned toward her before she begins. Often while I walked

through the forest or even over adjoining pastures, a female manakin has drawn attention to herself by her trilling and slow wing-beating. Sometimes, acting upon the hint she gave me, I have, after considerable searching, found a minute fledgling perching motionless amidst the undergrowth; but perhaps more often I have failed to find the birdling that was doubtless hiding not far off. If one follows the displaying manakin she will flit ahead to repeat her act again and again, always on some low twig. And while one searches through the vegetation she makes a point of coming in front of him to perform. If the ground is clean she may flutter slowly just above it; but I have never known any member of the manakin family to simulate injury on the ground. Wing-flitting is part of the courtship display of the male Blue-capped Manakin, but it is not accompanied by a loud snapping sound made by knocking together the thickened shafts of the remiges, as with other species of *Pipra* and with *Manacus*.

One day while I searched for nests through a dense thicket in southern Costa Rica, a bird that I had not seen startled me by bursting into action only a few feet away. A Cassin's Dove fluttered around me and came to rest on a branch about a yard above the ground. Here he—I infer the sex from the hour of the morning—slowly and deliberately beat his wings in a manner in no wise suggesting that he had suffered injury, but obviously calculated to attract my attention. When I moved nearer he flew off, skimming low over the ground, until he vanished amid the bushes. After his departure I found his nest, a shallow platform of fine twigs upon which rested a single unfeathered nestling, seven feet up and on the side of me opposite the scene of his display.

The Rufous-rumped Cuckoo is a terrestrial, ambulatory bird that dwells amid the cacti and thorny scrub of the more arid portions of Central America. Once, in the Motagua Valley of Guatemala, I had the good fortune to find its nest, a shallow dish placed on the ground beneath a low bush trimmed into rounded form by browsing goats. The incubating cuckoo allowed me to approach until my bent-over head was almost above it. Then it walked away with the greatest deliberation, taking little mincing steps, until it reached a bare, sandy place beneath an organ cactus. Here it paused, partially erected all its body-feathers, drooped its wings, spread and depressed its tail, then with the same slow, short steps moved back and forth several times over the bare ground. It did not flutter nor beat the ground with its wings as other birds do when trying to lure an intruder from the nest, yet its attitude served well to draw attention. As I approached, it slowly moved beneath some bushes and out of sight. Could this have been an example of the type of distraction display which ornithologists have since learned to call the " rodent-run "?

In a mossy bank on a steep, forested mountain-side in the Guatemalan highlands I found the oven-shaped nest of a lovely flame-breasted Slate-throated Redstart. The female would sit upon her three eggs until I came

within arm's length. A nearer approach would cause her to dart out, flying low, to settle on the ground or on a low perch close in front of me, where she would quiver her relaxed wings. If I followed, she would move off a few yards to repeat the act, and yet again, if need be, until at a good distance from the nest she winged away through the mountain forest without more ado. Her actions failed to suggest that she was injured, yet left little doubt that she tried to lure me away. This and other species of *Myioborus*—attractive wood warblers of the tropical highlands—may upon occasion act convincingly the part of an injured bird, but at other times merely quiver their wings.

The antbirds (Formicariidae) are a multitudinous family of small insectivorous birds restricted to the warmer parts of the Western Hemisphere, where the great majority dwell in the heavy tropical forests or among dense thickets. Brilliant colours are unknown in the whole great group; but many are most attractively clad in combinations of black, white, brown, chestnut, and shades of olive and grey. A number are equipped with concealed areas of white in the centre of the back or at the bases of the wings, more rarely on the flanks. In such parts of the plumage each feather has two colours, and the dark tips ordinarily overlie and conceal the white bases; but when these feathers are turned outward the white becomes conspicuous in unbroken areas. Similar concealed patches of white are found on some of the cotingas; they remind us also of the hidden areas of scarlet, yellow or white on the crowns of many American flycatchers. All these masked colours are displayed by their wearers in times of excitement, especially in amatory and bellicose moods.

Except for a few species that nest in holes in trunks, nearly all the antbirds built open nests—usually pouches or vireo-like structures—rarely lower than a foot or higher than 15 feet above the ground. Male and female take turns at incubation and, like so many of the duller denizens of the tropical forest, some of the antbirds sit very closely, allowing a man to come almost within reach before they quit the nest. Then they may drop to the ground, or to a low perch, and make display, into which enter the concealed patches of white. A male Tyrannine Antbird would sit motionless on the two eggs deep in the thick-walled pouch hanging above a rivulet at the edge of the forest. It required considerable shaking of the supporting grass-stems to make him depart. Then he would drop to a fallen log or the edge of the stream, conspicuously displaying a broad, snowy-white area in the centre of his blackish back. A female Spotted Antshrike would drop at my approach to the ground, where she grovelled on the dead leaves, beating her wings in an excellent act of feigning injury; while her mate, perching beside the nest and revealing a snowy area in the midst of his slate-coloured back, would repeatedly nip my intruding finger. I have never known any other pair of birds of any kind to combine in this fashion the attempt to lure the intruder from the nest with an active and spirited defence.

A pair of Slaty Antwrens had built their open cup of black fibres, four feet above the ground, in the fork at the end of a horizontal branch of a small sapling in the forest. While the female, as told above, would always vanish almost before I came within sight, her mate would remain steadfast to his duty while I approached and stood beside him, then drop from the nest and display. The performance was longest continued and most spectacular when I visited the nest on the morning the two naked nestlings hatched. After I had come within reach, the male antwren jumped from the nest and fell almost to the ground, but clung to a thin upright stem, where he spread and slowly beat his blackish wings, revealing small white epaulets ordinarily concealed. He continued so for a longer time than I had seen him do before the eggs hatched, then flitted to a similar upright perch a few feet farther from me, where he spread and beat his wings as before, but now for a briefer period. I followed, and he flitted from sapling to sapling ahead of me, trying to lure me on, sometimes allowing me to approach within three or four feet before moving to a more distant perch. Almost always he clung to upright stems. His wing-displays became briefer as he drew me farther from the nest, and at length ceased. When he had led me a good distance from his newly hatched babies he vanished amid the underwood and began to call his mate.

A male Bridges' Antshrike, whose nest was ten feet up in a sapling among tangled growth at the edge of the forest, would continue to cover the two eggs until I stood below and shook the little tree. Then he would drop almost to the ground before flying off. On the morning the first egg hatched he paused on a perch near my feet, where he spread and quivered his wings. Then he moved a short distance off and repeated the performance, as though trying to entice me to follow; but he displayed no hidden area of white.

4. THE " BROKEN-WING " RUSE.

Now that we have considered examples of conspicuous departure from the nest, when the bird failed to create the impression that it was injured or otherwise not fully in command of its faculties, we are in a better position to understand cases of injury-simulation proper. We have seen that the bird, far from being so torn between conflicting impulses that it was incapable of co-ordinated movements as it fled the nest, performed in many instances actions which must call for a higher degree of co-ordinated effort than its ordinary flight, if only because they are less habitual. When a bird acts as though injured upon being driven from the nest, is its behaviour the same in kind as that which we have already discussed, or do now the wholly new factors of panic terror and crippling indecision enter in?

Ground-nesting birds may begin their display of helplessness immediately upon leaving the nest, or they may retreat a short distance in their normal manner before they begin to act—just as we have seen among birds which

make a display that fails to suggest injury. Thus the Pauraque, a common goatsucker of tropical America, continues upon its eggs or young on the ground until an approaching man is almost upon it, just as it does at any season of the year while resting during the day. In either case it rises up lightly from almost beneath your feet, and goes flitting airily away. But if it has eggs or little ones to safeguard it may flutter to earth a few paces away, where it grovels among the brown dead leaves, pressing its breast to the ground, beating the earth with its wings, uttering the while low, soft, croaking sounds. Closely approached, it bounces lightly ahead a short distance and comes down to repeat its grovelling, wing-beating display, and so on, until it has led the intruder a safe distance away from its treasures. The act itself may indeed create the impression that the Pauraque is too distressed or too badly injured to move, and so may deceive an animal, but hardly a man who reflects upon the easy withdrawal that precedes each seeming paroxysm of helplessness.

Tree-nesting birds that simulate injury often drop almost or quite to the ground before beginning their act. Those who hold that the injury-feigning bird has not full control over its movements may see in this initial fall strong support for their theory. But birds of a number of species nearly always depart from the nest in this manner. The little blue-black and gold euphonias (*Tanagra*), upon sallying from their tiny oven-shaped nests, if they be high in trees, fall sharply, or even vertically, downward, sometimes almost to the ground, then curve gracefully upward and away. The Turquoise-naped Chlorophonia has the identical habit, as have certain tree-nesting wood warblers. A Barrot's Fairy Hummingbird that I watched would drop below her high nest before flying away. All of these birds left their nests spontaneously to hunt food, and were quite undisturbed. The prudence of such a mode of departure seems obvious. The little bird is most conspicuous, not as she drops with partly folded wings from her nest, but as she breaks her fall and begins to curve upward with slow initial velocity. It is at this moment that she would be most likely to draw the gaze of an eye which had the nest in its field of vision, but had not actually picked it out; and she would leave the watcher with an entirely erroneous impression as to her actual point of departure. The habit may be compared with that of birds which creep through the herbage upon quitting their low nests, first flying up and revealing themselves at a distance.

This initial drop was the principle of success in one of the most baffling and convincing acts of injury-simulation that I ever beheld. I had gone into the forest with a neighbour who had promised to show me a tinamou's nest. While I stood motionless, watching my guide, who had gone ahead to locate the nest more exactly, I suddenly caught sight, out of the corner of an eye, of a small, brownish-backed bird that appeared to spring up from my

very feet and fluttered painfully over the leaf-carpeted floor of the forest, here rather free of undergrowth, until it was lost to view among the foliage. I felt sure that I had trodden upon the bird's nest and injured her as she sat. But careful examination of the ground where I stood failed to reveal a nest. Then I noticed, slightly above the level of my head, in the small sapling beside me, and so close that I might have touched it without moving a step, a small, deeply cupped nest made of fine black fibres and sparingly covered with green moss on the outside, suspended by its rim between two horizontal branches—a typical antbird's nest. The owner had clung steadfastly to her single nestling with the huge monster standing so close beside her, until her courage reached the breaking point, then took her departure in the manner least likely to betray the position of her baby, at the same time doing what she could to lead that monster away. Returning later, the monster identified her as an Olivaceous Antvireo.

Whether a bird will unobtrusively vanish from her nest, try to lure the intruder away, or attempt an active defence, depends largely upon the nature of the potential enemy. The Whitebrowed Gnatcatcher took a conspicuous departure when I visited the nest but bravely attacked a small snake that threatened it. Where man is concerned, the Song Tanager is one of the most timid of birds, usually slipping from her nest while he is still a long way off; yet I once watched one of these birds attack a green snake far larger than herself that was eating her eggs. The Neotropical Kingbird attacks a hawk but flees from man. The Kiskadee treats man and large serpent alike, threatening both with bold darts and angry sounds. But as a rule the bird that attacks or makes feint of attack does not display the broken-wing ruse to the same kind of intruder; and those that practise the ruse on man do not try to defend their nest against him. Aside from the Spotted Antshrike, of which the female of a pair simulated injury while her mate attacked my hand, I have only thrice encountered exceptions to this rule.

On an afternoon in mid-August, while I walked slowly along an indistinct trail through the forest close by my house in Costa Rica, I met a Bicoloured Antbird who scolded while clinging to an upright stem close in front of me with a fat insect in its bill. When I started to look for the nest which this behaviour suggested, the bird darted angrily past me, so close that its wing brushed my legs. It scolded more, then, as I continued my search, dropped to the ground, where it grovelled, beating its half-spread wings against the fallen leaves. It repeated this again and again, always within a yard or two of me. Soon I found two pot-bellied, nearly naked nestlings lying on the ground close beside the remains of a low palm-stump, whose papery outer shell had collapsed, spilling out the nest which had been hidden in its hollow centre. This must have happened some hours earlier, for the young antbirds were already cold and sluggish, and one had a little blood on

its flank. About the time I found the nestlings the parent swallowed the insect that it had been holding in its bill; and now the character of its utterances changed. It incessantly called " per-r-r-r ", at once plaintive and protesting, and several times more lay flat on the ground, beating its half-spread wings against the fallen leaves. Each such demonstration was performed in a single spot, without fluttering along, and lasted only a few seconds. When I took the nestlings in my hand, which I held on the ground in front of the parent, it advanced and bit a finger, not once but three or four times, although so gently that I hardly felt it. Next I spread my handkerchief on the ground and laid the nestlings on it while I considered what to do with them, then improvised a nest in a hollow leaf-sheath of chonta palm. This took ten minutes or more, and all the while the parent lay or sat motionless on the ground less than a yard away from the handkerchief with the nestlings, intently watching or guarding them. After placing the youngsters in a substitute nest, that provided shelter from the hard rains of this season, close by the ruined one, I went away. Returning next morning, I found them dead, apparently because they had not been brooded. It is just possible that this was because their mother, who would have attended the nest through the night, had lost her life in whatever disturbance caused the collapse of the nest; for the sexes of the Bicoloured Antbird are indistinguishable and I had seen only one. The confidence of the parent in my presence is not so surprising when it is recalled that this antbird is very tame; and sometimes one has followed me for a long distance through the forest, snatching up insects stirred up by my passage, and often coming within a yard of my feet. At my second nest of this species, found the following year not far from the site of the first, both parents repeatedly gave the distraction display when I visited their eggs, and more energetically on the morning their nestlings hatched.

A Yellow-thighed Sparrow of the Costa Rican highlands had built her nest among tall, densely matted grass leaning over a bank beside a path that ran between a pasture and the forest. To see the contents of the nest I would stand in the pathway below and hold up a mirror. The bird was from the first most steadfast in her attachment to her nest, allowing me almost to touch her before she hopped from the two eggs and flew down to the bushes at the edge of the forest. On the day the two nestlings hatched she was even bolder, permitting me to touch her with my upraised hand. Then she rose from the nest and turned about to face me, with one wing lifted high in an attitude of defiance. Next, perhaps deciding that I was too big to be intimidated so, she dropped down to the pathway almost at my feet and hopped across it to the woods with her wings raised above her back, seemingly trying to lure me to follow; but she did not feign injury in a convincing manner. From the margin of the forest she flew back to the

grass where her nest was concealed, where she incessantly reiterated a sharp note of distress.

A White-fronted Dove entertained me with a far better act, both in its first and second scenes. Her nest was about nine feet up in a small tree in a little coffee plantation. I wished to learn what it contained, again with the aid of a mirror. Shaking the tree did not cause the brave dove to move; and when I touched its tail with the end of the withy to which I intended to attach the mirror, it merely raised its wings straight above its back in an attitude of defiance, revealing the beautiful cinnamon of the under wing-coverts. When I again attempted to touch the dove with the withy it brought down its right wing upon it with a resounding whack.

Thinking that I might glimpse the contents of the nest when the bird rose up in a defiant attitude, without making it fly off, I now attached the mirror to the rod and raised it toward the dove. When the mirror reached the level of the nest the bird suddenly dropped to the ground, where it began to move away, hopping and limping, quivering its wings and vainly beating them. It was easy to believe that when it struck the stick it had broken a wing and was unable to fly. The weeds in the plantation had just been cut, leaving the ground clean and free of obstructions, an excellent stage for the bird's act. I followed at a walking pace; the dove, all the while moving with an appearance of the greatest agony and distress, easily maintained a distance of fifteen or twenty feet ahead of me until it reached the edge of the plantation, two hundred feet—I measured it later—from the starting point. Here the dense growth of weeds and bushes perforce put an end to its demonstration, and it was obliged to fly over the barrier into the thicket beyond. But chancing to find a log in plain view of me, it alighted here and resumed its helpless wing-flapping, as though to lead me still farther away from its already distant nest. But the tangled weeds made it impossible for me to follow; and after a minute of this acting the dove vanished amid the dense vegetation.

Returning to the dove's nest, I again raised the mirror, and was greeted by the reflected image of a single half-grown nestling. I have never on any other occasion seen a wild pigeon defend its nest so bravely, or make so realistic and long-continued a display to lure away the intruder. The White-fronted Dove, like the Yellow-thighed Sparrow, far from going into a fit or becoming hysterical, was sufficiently in possession of its wits to change its tactics and try the broken-wing ruse when it saw that menace failed to meet the exigencies of the situation.

At a lower nest of a White-fronted Dove the parents would also allow a very close approach before they fled. One day one of them permitted me to come within reach, and as I was on the point of touching it with my hand, dropped to the ground and fluttered madly away as though mortally wounded and in great agony. A few moments after the departure of the parent the

nestling, although barely feathered and not yet able to fly, jumped from the nest and attempted to escape by fluttering over the ground. I easily caught and returned it to the nest, where, after it had become calm, I persuaded it to stay. On every subsequent visit, even during the warmest hours of the day, I found one of the parents brooding the now completely feathered nestling, whose head and neck usually projected from beneath the parent's breast. Five days after the episode we have just narrated, I again advanced a little nearer than was my custom. The brooding parent at first crouched over the nestling, but under my continued scrutiny became alarmed, jumped to the ground, and dragged itself away with a tremendous flutter of wings all out of proportion to its slow progress. Then the nestling winged away in the opposite direction. It now flew well, and did not pause until it had passed from my view among the bushes. The conspicuous withdrawal of the parent served to divert attention from the fledgling's silent departure.

The display of the first White-fronted Dove leads us to consider another characteristic of the injury-feigning act. We saw in the case of the Pauraque that it might begin, not the instant the bird leaves the nest, but after a brief delay, while she moves to a spot more convenient for her performance. Now we learn that it may also be discontinuous, the bird displaying until it reaches the end of the terrain suitable for its act, then resuming when it encounters another promising spot. Sometimes the bird, after having passed into dense vegetation in her efforts to lure away the intruder, returns again to its edge to repeat her display. I have seen such behaviour on the part of the Slate-throated Redstart. I think it fully as likely that her continuing performance is motivated by the vanity which prompts the repetition of a successful act as caused by hysteria or a disabling conflict of impulses.

If a bird finds near its nest only a small clear area surrounded by dense vegetation that would impede and conceal its movements, instead of leading a straight course from the nest it may move back and forth across its narrow stage, in full view of the unwelcome audience. Last year I watched a male Olivaceous Antvireo, driven from newly-hatched nestlings by my daily visit, turn repeatedly to stay within the small clear area amid the undergrowth, where he grovelled in seeming agony, beating against the leafy ground dark wings that revealed next the body white bands that I had not previously seen.

While the great majority of birds that simulate injury upon quitting the nest wait until the intruder is nearly or quite within reach of it, a few kinds advance to meet the danger while still a long way off—like the good strategists they are. Here, placing themselves in front of the interloper, they behave as though helplessly injured, and so feigning, usually manage to lead him still farther from the nest, and utterly confuse him as to its true

position. I have never witnessed such behaviour, which is most commonly seen in the plover family. For example, Taverner (1936) describes the behaviour of a Killdeer which nested on the open prairie in Manitoba :

" If a horse or a cow grazed too near, the bird lay low until almost the last minute and then flew suddenly into its face with a great outcry. The animal invariably staggered back at the unexpected onslaught and circled the spot in confusion, while the bird, its object accomplished, after a few dives and expostulations returned quietly to its nest. However, when a man or a dog approached, it flew to meet him from afar, indulged in all the broken-winged helplessness with which we are familiar and led the enemy far from the nest before returning to it. The two schemes of action happened too often that summer to be the result of casual accident. The reaction in respect to the dog was particularly interesting. The dog, slavering and all excitement, pursued the bird closely. Every moment we expected to see its jaws close upon its expected prey, but each time that prey escaped by a margin so small that hopes of success were raised rather than dampened and the chase was hot. As they drew away from the immediate neighborhood the bird took less and less chances until finally the dog was tearing futilely around far from the point of encounter and evidently without thought of returning to it."

Allen (1936) described in detail how the injury-feigning Killdeer creates the impression that it is lying helplessly on its back while actually it rests on its belly. He pointed out that " it would obviously be of use to the bird thus to deceive its enemies, whereas actually to turn on its back would make a getaway difficult ".

5. INJURY-SIMULATION NOT ORIGINATING AT THE NEST.

Thus far we have been concerned chiefly with injury-simulation by birds that had just been driven from their nests or, more rarely, had left their nests to advance and meet the intruder. But birds whose incubating or brooding has not been interrupted may at times simulate injury or otherwise display. They may arrive at the nest and, finding a supposed enemy there, attempt to lure him away. Or their young may already have left the nest and be threatened by danger which the parent attempts to divert from them in this fashion.

Following the parents as they carried food, I had found a nest of the Chestnut-sided Warbler, situated three feet above the ground in a cornel bush on a scrubby hillside above Cayuga Lake, in the State of New York. It contained two half-grown Cowbird nestlings which squealed a little as I took them in hand, and drove the foster-parents to frenzied efforts to entice me from the nest. The male warbler fluttered from twig to twig in front of me, vibrating his wings and spreading his tail; while his mate descended to the ground beneath the dogwood clump, where she crouched on the dead leaves with vibrating wings and spread tail, moving forward slowly and lamely after the usual manner of distressed parent-birds. I squatted down in the midst of the bushes the better to see her, and the male, becoming uncommonly bold and loudly chirping his protests, displayed so close

before me that every delicate marking of his plumage was visible: the golden crown, the white cheeks, the rich chestnut bands along the flanks and sides, and every streak of black and white and grey on the wings and back and tail. I might have reached forward and touched him had he only remained still. On the following day the performance was repeated for my benefit.

During that same summer I was led by the excited chirping of a pair of American Redstarts to the discovery of their nest in the crotch of an elderberry bush about nine feet above the ground. When I attempted to learn by feeling with a finger-tip what it contained, the birds gave such a demonstration as I have rarely witnessed. The female Redstart approached the closer to me, advancing within easy reach as she chirped her distressed reproaches; but the male, although he kept a somewhat greater distance, was the more active in his efforts to lead me away. He perched on a low twig with tail spread and wings fully extended, vibrating—it seemed to me—as rapidly as a hummingbird's. What a splendid colour-contrast in the full black and orange-salmon of the wings flashing into a blur, while the rich colours of the relatively motionless tail showed so clearly! Descending to the broad surface of a skunk-cabbage leaf, he continued his manifestations of distress. Next, falling to the ground, he danced over it with spread tail and fluttering wings; but it impressed me rather as some fairy dance than as a wounded bird attempting to divert grave danger from his offspring. The female Redstart's display was similar but less intense; and her paler colours made it less spectacular. When at length I returned my attention to the nest, I found it empty. Since it is not likely that the birds should have become so excited over an empty nest, I had no doubt that fledglings were hiding close by, possibly having scrambled to safety while my delighted eyes were fastened upon their parents. A nearby pair of Redstarts made no such demonstration when I visited their helpless nestlings.

Selous (1927) described the behaviour of a wild Mallard duck with seven well-grown ducklings, upon which he came among the Dutch polders. At first the ducklings lay perfectly still, pressed together, until he stooped and touched one, when they scattered with plaintive pipings in all directions, as though he had touched them all at once. The mother duck then ran out in front of him and struggled over the ground as if unable to fly. He followed, running after her, until she had led him a good distance off. After that the duck followed Selous, keeping a wary eye upon him, lest he return and again molest her brood. Grey of Fallodon (1927) gave a vivid account of how a parent English Partridge, by a timely display of the broken-wing ruse while two downy chicks that had lagged behind crouched at his feet, so successfully diverted his attention that these youngsters scuttled off unseen, although he did his best to keep them in view.

The most protracted distraction displays that have come to my attention were given by parent birds which had not been driven from the nest just before they began. While Moreau and Moreau (1937) were examining the nestlings in a frail, low nest of the shrike *Nicator chloris* in the tropical African forest, their presumed mother arrived and dragged herself about through the ground litter, fluttering helplessly, and continuing this wonderful display for a quarter of an hour. On 6 August 1946 I witnessed an amazing demonstration by a female Whip-poor-will in Michigan. As I descended a leaf-strewn slope with scattered low trees and bushes, the goatsucker arose from the ground where she had been resting and alighted on the upturned end of a fallen branch, five or six yards ahead of me. Here, perching crosswise about a foot above the ground, she puffed out her feathers and uttered a fairly loud, long-continued hiss, punctuated at intervals by a throaty note that suggested the first syllable of the usual " whip-poor-will " call. At the same time she relaxed her wings, brought them forward until they almost met in front of her breast, and beat them rapidly, making the barred primary feathers strike against the dead branch where she rested. For several minutes she continued this vigorous demonstration, the picture of anguished parenthood, then moved to another perch to resume it. While I continued to stand in the same spot, the Whip-poor-will circled around me, always alighting on a branch within a yard of the ground to continue her hissing, moaning and vigorous wing-shaking. How long she might have continued this display I do not know, for after she had been performing tirelessly for about 15 minutes I left in compassion for her evident distress. Near the point whence she first arose was a single egg, cold and wet, which later proved to be infertile. When on subsequent visits to the same spot the female goatsucker displayed as before, yet was never seen to rise from the egg, we began to suspect that she had a youngster that had hatched from the other egg of the usual set of two, and after a little searching found a downy Whip-poor-will, about a week old, resting on the ground about 25 feet away. On two of our visits the female, who was moulting, led us for about 150 feet, displaying on successive perches as she flitted ahead of her advancing visitor.

6. SYMPATHETIC INJURY-SIMULATION.

Sometimes, when the parents of threatened young birds pretend a broken wing to lure away a trespasser, neighbours of the same species, whose offspring are in no immediate danger, will be simultaneously stricken with the same infirmity, and all together indulge in antics that tend to distract the intruder's attention from the little ones. Chisholm (1936) wrote that " in Australia this joining of forces has frequently been observed among certain Chats and Honeyeaters; when a pair of nesting birds flutter along the ground and utter

distressful cries they are sometimes reinforced by other birds of the same species (which may or may not be nesting), and the whole company feigns injury". Similar behaviour has been described for the Hooded Warbler (Grimes 1936), the Semipalmated Plover (Swarth 1935), the New Zealand Pied Stilt and a pratincole in India (Armstrong 1947). I regret that I have never myself witnessed sympathetic injury-simulation.

(TO BE CONCLUDED.)