

ON THE BREEDING BEHAVIOR
OF THE COCK-OF-THE-ROCK
(AVES, *RUPICOLA RUPICOLA*)

E. THOMAS GILLIARD

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 124 : ARTICLE 2 NEW YORK : 1962

ON THE BREEDING BEHAVIOR OF THE COCK-OF-THE-
ROCK (AVES, *RUPICOLA RUPICOLA*)

ON THE BREEDING BEHAVIOR OF
THE COCK-OF-THE-ROCK (AVES,
RUPICOLA RUPICOLA)

E. THOMAS GILLIARD

*Associate Curator, Department of Ornithology
The American Museum of Natural History*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 124 : ARTICLE 2 NEW YORK : 1962

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 124, article 2, pages 31-68, text
figures 1-6, plates 29-38

Issued July 16, 1962

Price: \$1.75 a copy

CONTENTS

INTRODUCTION	37
Acknowledgments	39
The Expedition	39
Methods, Procedures, and Recording of Data	40
The Kanuku Mountains	41
Meteorology and its Cyclic Effects	41
Rainfall	41
Seasonal Events	41
Area Reconnoitered	42
PRIMARY STUDY AREA	43
THE DISPLAY TERRITORY	46
The Defended Territory	46
Primary Display Stages of Individual Male	48
Secondary Display Stages	48
Tertiary Display Stages	49
Waiting Stages	49
THE STUDY POPULATION	50
Display Paraphernalia	50
Orange-Red Coloration of the Cock	51
The Bower as Component of Display Paraphernalia	51
Components of the Display	52
Vocal Display by Males	52
Vocal Display by Females	52
Mechanical Noise Displays by Males	52
Movement Displays	53
Static Terrestrial Displays	54
Head-tilting Posture	54
Head-over-Shoulder Posture	54
Eye-catching Movements Associated with Static Postures	54
Annual Periodicity and Daily Rhythm of Display	54
Effects of Weather	55
Interactions Among Adult Males	55
Interactions Among Males and Females	56
Interactions Among Adult and Immature Males	56
THE NESTING TERRITORY	58
SPECIMENS COLLECTED	60
Nest	60
Male	60
COMMENTS ON THE DISPLAY OF <i>Rupicola rupicola</i>	61
Sign Stimuli Received from Habitat	61
Sign Stimuli Between Males	61
Sign Stimuli Received by Female from Male	61
Sign Stimuli Received by Male from Female	62
EVOLUTION OF ARENA DISPLAYS	63
TAXONOMIC CONCLUSIONS AND SUMMARY	66
BIBLIOGRAPHY	67

INTRODUCTION

ARENA BEHAVIOR is a highly advanced and relatively rare form of avian courtship behavior. The males of the species that have adopted this behavior are polygynous. During the breeding season they usually live in bands or clans in the vicinity of long-established mating stations, or "arenas." There they perform elaborate dances that serve the dual functions of establishing the breeding hierarchy and of signaling prospective mates. In arena birds, no lasting attachments are formed between the sexes, and the males play no part in the rearing of the young. Unlike the arena-behaving species, the vast majority of the birds of the world cling to primitive patterns of courtship behavior (see Kendeigh, 1952, p. 279) in which a pair bond develops between a specific male and female, and the pair then shares to a greater or lesser extent the raising of the young. In the more advanced groups the males sometimes tend to do little more than defend the nest. But apparently in every case in which there is a pair bond, there is a sharing of the work connected with the rearing of the young.

In arena birds, however, there is no pair bond and no sharing of the work. In such species an abrupt shift in habits has occurred, with the males and the females in some species living apart for all but a few hours, or even minutes, per year.

Because this curious shift has occurred in unrelated species in widely scattered parts of the world, one must assume that it has special adaptive values. Some of the well-known arena birds are the Ruff, some hummingbirds, some pheasants, and some grouse; among passerine birds, arena-displaying forms are known in some of the birds of paradise, some bowerbirds, some weaverbirds, some manakins, and in one cotinga.

Very little is known concerning the manner in which arena behavior originates and operates in evolution. One theory is that of Armstrong (1947, p. 245) who suggests that "the ceremonies of [arena birds] may be adaptations to meet the problems arising from a differential sex ratio between the members of each sex contemporaneously in an effective

breeding condition, or, in some cases, an actual differential sex ratio."

I have had the opportunity of studying under natural conditions the arena behavior of five species of birds of paradise (*Paradisaea apoda*, *P. minor*, *P. raggiana*, *Pteridophora alberti*, and *Diphyllodes magnificus*), two species of bowerbirds (*Archboldia papuensis* and *Chlamydera lauterbachii*), and one species of manakin (*Chiroxiphia pareola*). In order to understand this perplexing behavior better, I was anxious to make comparative studies of the Cock-of-the-Rock (*Rupicola rupicola*), the cotinga in which arena behavior had been discovered. However, to my surprise, I found that no modern field studies of this species had been made. The report of Robert Schomburgk, who discovered arena behavior in the Cock-of-the-Rock, proved to be the most specific and detailed, yet that report was based on very brief observations made during a day of heavy travel on February 8, 1839, while Schomburgk was crossing mountains comprising the height of land between the Orinoco and the Amazon basins in what is known today as the Guiana Highlands. He was attempting to go from the headwaters of the Essequibo River system to Esmeralda on the upper Orinoco, and at the time of his discovery he was near Mt. Waraima. This mountain appears on Schomburgk's map as about four-fifths of the way toward Mt. Duida on a straight line from Mt. Roraima.

Robert Schomburgk's report (1841b) elicited wide interest among early naturalists, and it has since been widely quoted. For example, Darwin (1871, p. 83) quoted it as follows: "The male [*Rupicola rupicola*] is one of the most beautiful birds in the world. . . . Schomburgk has described [the] courtship; he found one of their meeting places where ten males and two females were present. The space was four to five feet in diameter, and appeared to have been cleared of every blade of grass and smoothed as if by human hands. A male was capering to the apparent delight of several others. Now spreading its wings, throwing up its head, or opening its tail like a fan; now strutting

about with a hopping gait until tired, when it gabbled some kind of note, and was relieved by another. Thus three of them successively took the field, and then, with self-approbation, withdrew to rest."

Robert Schomburgk, a geographer, had been commissioned by Queen Victoria to explore and map British Guiana. The King of Prussia commissioned his brother Richard, a botanist-ornithologist, to accompany Robert on his later trips. Thus it came about that in 1841 Richard Schomburgk visited the Kanuku Mountains and observed the Cock-of-the-Rock. Richard, in his report of his travels in British Guiana (1922), confirmed Robert's discovery of the arena displays. He described this event, which he witnessed near the summit of Mt. Ilamikipang (see pl. 31, fig. 1, and pl. 32, fig. 1), as follows: "The higher we climbed the more difficult became the track and the oftener we were obliged to take a rest: while thus engaged we suddenly heard the well known note of the Cock-of-the-Rock at not too great a distance. My companions immediately sneaked with their weapons in its direction, when soon after one of them returned and told me to follow him carefully and lightly. We might have crept some thousand paces through the bush on hands and knees when . . . on crouching down quietly beside the Indians, I witnessed the most interesting sight. On the smooth surface of a rocky crag a party of the most beautiful birds were keeping up a dance; a performance that had been doubted by many ornithologists though not only my brother, but many of the Indians had already told me plenty concerning it. While about a score of birds perched upon the bushes surrounding the play-ground, were uttering the most peculiar notes, and apparently constituting an admiring audience, one of the males was cutting capers on the smooth boulder: in proud consciousness of self it cocked and dropped its widespread tail and flapped its likewise expanded wings, and thus continued to figure out the steps until it seemed to be exhausted, when it flew back on the bush and its place was taken by another male. The female in the meantime uttered a peculiar note, watched unweariedly and on the return of the tired performer uttered a scream denoting applause."

A number of travelers subsequently mentioned finding the peculiar clearings. A collector, W. Frost (1910, p. 314), and a botanist, Nicholas Guppy (1958, p. 91), reported having observed the cocks-of-the-rock dancing on their ground courts, but their observations added little to what had already been reported by the Schomburgks.

At least two attempts were made to study and photograph the courtship behavior of the Cock-of-the-Rock. In 1937 the entomologist John Meyers visited the Nappi region in the northern Kanuku Mountains with E. E. Melville, who in the early 1930's had observed display grounds there. Melville informed me that he and Meyers found cocks congregated in trees over a group of ground clearings, where he had earlier observed them. The two men erected a blind and installed cameras, but unfortunately Meyers was attacked by ants, the bites of which so sickened him that he called off the venture.

In 1960 David Snow and his wife made a brief attempt to study and photograph the arena displays of the Cock-of-the-Rock at a display ground which they visited with James M. Fowler, the American falconer. Unfortunately they arrived on the scene at the wrong season, and the males were not observed on the ground, but they found a nesting cave.

In November, 1960, the writer had the good fortune to meet Fowler at the American Museum of Natural History. During Fowler's explorations in search of nests of the Harpy Eagle in the Kanuku Mountains of southeastern British Guiana, his Macusi Indian guides had shown him display grounds of the Cock-of-the-Rock. Mr. Fowler very kindly supplied the names of two Indians who, he believed, would be able to guide the writer to display grounds in these mountains, and he "hazarded the guess" that February and March were the months when *Rupicola rupicola* would most likely be in attendance at its dance grounds.

The writer transmitted this information, together with an expedition prospectus, to Dr. Dean Amadon, Chairman of the Department of Ornithology, and to Dr. James A. Oliver, Director of the American Museum of Natural History. With their enthusiastic approval and the support of the American

Museum of Natural History, he then submitted a request for financial support to the Committee for Research and Exploration of the National Geographic Society. This request was granted very promptly, so that the studies reported upon herein could be made during the breeding season of 1961.

ACKNOWLEDGMENTS

I am greatly indebted to Mr. James M. Fowler for his generosity in supplying me with geographical information and the names of responsible guides. I must also extend warm thanks to Dr. and Mrs. David Snow for their thoughtfulness in sending me nesting data which they obtained in late March, 1961, when they revisited the nesting cave reported on herein and found eggs in nest 4 (pl. 37, fig. 1). I am also deeply indebted to Mr. Melvin M. Payne and to the other members of the Committee for Research and Exploration of the National Geographic Society for hastening my grant so that I could begin my explorations a full year earlier than I had anticipated. I am deeply indebted to Drs. Wesley E. Lanyon and Kenneth R. John for their kindness in reading the manuscript and offering many valuable suggestions, and to Mrs. Margaret Gilliard for her splendid drawings.

In Georgetown I was graciously received by His Excellency Sir Ralph Grey, K.C.M.G., K.C.V.O., O.B.E., Governor and Commander in Chief of British Guiana, and by Mr. Vincent Roth, Director of the British Guiana Museum. Mr. Ram Singh of the Museum staff and Mr. Roy Hewson of the St. Ignatius Livestock Research Station, Rupununi District, also helped me in Georgetown, and Mr. Hewson later assisted the expedition in the field. Mr. J. B. Bamford, Commissioner of the Interior, and Mr. Neville Franker, the Rupununi District Commissioner, were very helpful in their assistance to the expedition. I must also thank Mr. J. A. Sweetman of the Cartogeographical Division of the Department of Lands and Mines for making available much-needed maps.

At Lethem the expedition was fortunate to receive the assistance of Mr. Edward E. Meville, one of the pioneers. Mr. Meville, who has an extraordinary knowledge of the local Indians and of the region, is himself

part Macusi Indian. He arranged for our local transportation, carriers, and guides.

THE EXPEDITION

The aims of the expedition were threefold: to determine the exact nature of the social displays employed by *Rupicola rupicola*; to see if ethological evidence would shed new light on the relationships of *R. rupicola*; and to discover, if possible, the way in which arena behavior originates, develops, and operates in evolution.

The expedition party consisted of the author and four Indians of the Kanuku Mountain region. E. E. Melville acted as expedition agent in the little border town of Lethem. An African-Macusi, Alfred Jonas (Atti), of Moco Moco Village, a man of about 38 years of age who is widely regarded as the best woodsman in the Kanuku Mountains, served as guide. Atti was, in fact, the only person encountered who knew the locations of dancing arenas. He showed two to the expedition, and a third was discovered on the summit of Mt. Ilamikipang. An Arawak Indian, Joseph Cachon, 50 years old, for the last 21 years a farmer in the upper Kumu Creek region at the western foot of Mt. Ilamikipang, served as cook (and guide in the Mt. Ilamikipang area). Two Macusi Indians, Pedro Railyan and Laurence Gregory, served as general assistants and carriers.

The itinerary was as follows:

FEBRUARY 3: Flight by British Guiana Airways from Georgetown to Lethem.

FEBRUARY 3 TO 6: Lethem, preparing for field trip. Observations of local birds were made in neighboring savannas between Lethem and Moco Moco Village, along the edges of savanna lagoons, and along the edges of the Takutu River.

FEBRUARY 6: Lethem to Camp 1, on the north bank of Fly Creek. This camp was a quarter of a mile from ground display area 1 and nesting cave 1.

FEBRUARY 6 TO 27: Camp 1 (500 feet). Numerous short exploratory trips were made from this point in an unsuccessful attempt to discover additional display or nesting areas in the Fly Creek region.

FEBRUARY 27 TO MARCH 4: Camp 2 (400 feet), on the farm of Reginald McConnell, upper Moco Moco River Valley. Exploratory trips were made from this camp into the mountains to the northeast. A display area (no. 2) was discovered on a forested mountain top on March 1 at about 1800 feet. A nesting cave (no. 2) with a nest and a

female in attendance was discovered near this camp on March 3. Many general ornithological observations were made in this area.

MARCH 4 TO 7: Camp 3 (400 feet), at the western foot of Mt. Ilamikipang, on the Chacon farm. Many general ornithological observations.

MARCH 7 TO 9: Camp 4 (2700 feet), summit of Mt. Ilamikipang. This camp was reached by way of the old Macusi Indian trail used by the Schomburgks. This poorly marked trail crosses the range through a notch situated just south of Mt. Ilamikipang. Display area 3 was discovered on the summit of Mt. Ilamikipang.

MARCH 9 TO 10: Camp 3.

MARCH 10 TO 13: Lethem, reconnoitering by vehicle with Roy Hewson.

MARCH 13 TO 15: Camp 5, Jawari Lake, some 12 miles southeast of Lethem. Many ornithological observations.

MARCH 15 TO 16: Lethem.

MARCH 16: Long reconnaissance by vehicle with E. E. Melville to the Nappi River and to the Pirara flats at the northern end of the Kanuku Mountains.

MARCH 17: Flight by British Guiana Airways from Lethem to Georgetown.

METHODS, PROCEDURES, AND RECORDING OF DATA

Except for one male of *Rupicola rupicola*, there was no collecting of birds. The collection of data was limited to field observations preserved in written form, photographic records, and tape recordings.

The written record consists of a series of timed-on-the-spot observations, which were entered in a small pocket notebook as the events unfolded and were transcribed and elaborated a short time later.

Eight-power Hensholdt binoculars were used for observations, as were the finding mechanisms of the two reflex cameras noted below.

The photographic record on still film was made with two M3 Leicas and a series of five lenses ranging from a standard *f*.2 50-mm. Ernst Letiz to an *f*.5.6 300-mm. Heinz Kilfitt telephoto lens. All but the 50-mm. pictures were shot with the aid of a Leitz reflex housing. A few exposures were made with the aid of supplementary flash, with a Kalart 2 lamp gun and F.P. 26B Blue Dot bulbs.

The photographic record on moving picture film was made with a 16-mm. Arriflex powered with disposable 7½-volt Burgess ignition batteries (No. 4F5H). The Arri-

flex lenses used in this operation were an *f*.1.5 25-mm. Schneider-Kreuznach Zenon, an *f*.2 50-mm. (same make), an *f*.2 75-mm. (same make), an *f*.3.5 150-mm. Heinz Kilfitt München Kilar, and the *f*.5.6 300-mm. Heinz Kilfitt München Tele-Kilar listed above.

Other photographic equipment used with the still cameras was: an *f*.4 90-mm. Leitz GMBH Wetzlar lens, an *f*.4.5 135-mm. Leitz GMBH Wetzlar lens, an *f*.4.5 135-mm. lens (same make), an *f*.4.5 200-mm. lens (same make), and a Leitz-Wetzlar bellows attachment.

Both the still and the motion picture cameras were operated from a Linhoff tripod equipped with a "Miller head." Two Weston Master III universal exposure meters were used.

The following types of film were used: Still film: 35-mm. Kodachrome (36 exposure rolls) Daylight film and 35-mm. High Speed Ektachrome (36 exposure rolls). Moving picture film: 16-mm. Kodachrome film in 100-foot spools, and 16-mm. Ekatchrome E.R. film.

Some 2000 feet of the Ektachrome E.R. film (with a film speed of A.S.A. 160) were exposed at a speed of about 16 frames per second. This footage lends itself very well to laboratory studies of the timing of the displays. Relatively little footage of the 16-mm. Kodachrome (with a film speed of A.S.A. 10) could be exposed owing to lack of sufficient light on the display grounds. The footage that was exposed was run at very slow speeds (usually about 10 to 15 frames per second) and therefore the action sequences were speeded up. Nevertheless, this footage is useful for laboratory analysis of the chronology of display movements. All the moving picture film was on 100-foot spools, and the longest continuous "run" was therefore of that length. However, owing to the extremely static quality of the displays, most of the films were exposed in shorter sequences.

All this film has been studied repeatedly by the writer. Certain actions and sequences of actions not noted in the field are discernible in the films and the displays are much easier to interpret through reference to the film than they were in the field. Furthermore, by repeated examinations of peculiar segments of the display, I have been able to decipher and describe some of the asymmetrical activities

by the displaying males, particularly lek activities that were rare and of slight duration.

A small Kodak Startech medical camera was used to make color shots at distances of 4 to 16 inches of small objects such as insects and flowers.

Sound recordings were made with a portable Trans Magnemite transistorized tape recorder (Model 612 E.V., serial no. 8057), manufactured by the Amplifier Corporation of America. Tapes were run at speeds of 15 inches per second. Long-recording Mylar audiotapes containing 900 feet of tape, with a running time of 24 minutes, were used. An Altec microphone with an extension cable permitted close-up recordings when the microphone was buried in leaves near the ground display areas.

THE KANUKU MOUNTAINS

METEOROLOGY AND ITS CYCLIC EFFECTS: For the following summary, information has been taken from native sources and from the annual meteorological reports for the years 1957, 1958, and 1959, from the Department of Meteorology of the British Guiana Government. The unofficial information was supplied chiefly by Atti, who possessed a remarkable fund of knowledge concerning the Kanuku Mountain region, based on first-hand observations made during a period of more than 20 years spent largely in the field, and on second-hand information passed down to him by word of mouth by his Macusi Indian elders. Atti spoke understandable English but, beyond being able to sign his name, could not write.

RAINFALL: Below are given the measurements (in inches) of the monthly rainfall recorded at the St. Ignatius Livestock Station, which is located near the Takutu River and about 1 mile south of the border town of Lethem. They probably reflect closely the rainfall conditions that exist in the Kanuku Mountains some 15 miles away.

	1957	1958	1959
January	0.57	0.08	0.25
February	0.34	1.05	0.19
March	None	1.74	0.03
April	1.11	13.58	3.06
May	10.90	8.27	5.11
June	18.15	14.05	16.63
July	11.84	7.36	11.64

August	10.01	12.66	6.26
September	0.05	0.45	5.21
October	0.84	0.16	1.96
November	0.14	0.06	2.25
December	0.25	0.01	0.14

SEASONAL EVENTS: Atti informed me that, in the Lethem-Kanuku Mountain area, "winter" occurs in February, "spring" occurs in May, "summer" occurs in September, and "fall" occurs in December. The period of almost continuous savanna fires and of occasional forest fires is in January and February. The period of least cloud cover is in February. The hottest month of the year is also February; the coldest is June. The heaviest winds occur in January; the quietest period of the year is in August. The heaviest rains fall in June. The period of highest water in the rivers, creeks, and swamps is in July, but the rivers begin to rise in late May. The period of maximum high water holds for about two weeks, and at that time the vast Pirara flats and neighboring regions at the headwaters of the Rupununi and the Rio Branco systems are inundated by several feet of water and resemble giant lakes. At such times it would be possible to pass by small boat over the height of land, thus crossing from the Amazon to the Essequibo River system.

The period of greatest insect abundance is in June and July; the period of least abundance is in September. The period of greatest abundance of flowering trees, grassland flowers, and new leaves is in May. The greatest number of trees have shed their leaves in February.

Most species of birds begin to nest in May. At this period, Atti said, there is a sudden surge of nesting activity both in the forests and in the savannas. He has found tinamous nesting in April, harpy eagles and ducks nesting in May, herons in May and June, and hummingbirds "as late" as July. Atti spoke also of a large bird rookery west of Nappi called Moninvui where thousands of long-legged wading birds begin nesting in May and June and continue in the area until the young leave in September.

May and June, Atti said, are the months when the tapir and the jaguar, as well as most of the quadrupeds, are likely to bear young. The *labaria* (fer-de-lance) may have its young in March, but most of the snakes of the

Kanuku Mountain region have their young in May.

AREA RECONNOITERED: The general area surveyed for the Cock-of-the-Rock is centered at about latitude $3^{\circ} 15' N.$ and longitude $59^{\circ} 45' W.$ It is situated along some 15 miles of the northwestern slopes of the Kanuku Mountains west of the Rupununi River and is between the elevations of 350 and 2700 feet. The area of primary study is drained by Fly Creek and the Menari River (pl. 31, fig. 1). The latter is a tributary of the Takutu, which, in turn, flows to the Atlantic via the Rio Branco and the Amazon. In general conformation, the northern foothills of the Kanuku Mountains are deeply eroded, with many huge rock falls and cliffs. The range, which is highly fragmented, is almost completely covered with forest, whereas the lowlands surrounding it to the north and west are chiefly savanna grassland dotted with trees and bushes. When viewed from any distance out on the savanna, the Kanuku Mountains thus resemble a forested oceanic island with a jagged crest.

The expedition, during its work in the area defined above, made three probes into the mountains in search of the dancing and nesting grounds of *Rupicola rupicola*. The first, the primary study area, was in the Fly Creek region, where a trail led into the forest about midway between Nappi and Moco Moco villages near the site of a very small, abandoned, Indian settlement. From a careful study of Richard Schomburgk's journal, the present writer is of the opinion that this abandoned settlement is the place where, in 1850, Schomburgk emerged from the forest after his walk from Nappi (Richard Schomburgk, 1922, p. 341). The present writer had a stone monument erected at the site, and this monument was used as a control point in the "pace" mapping of the region leading to and surrounding the main study area (see upper left corner of fig. 1). The expedition explored the slopes of the range in this area to an altitude of about 1000 feet in search of additional nesting and display grounds, but none was discovered.

The second probe was made into the mountains lying behind the Indian village of Moco Moco. The trail mouth leading into the forest at this point was near the confluence

of upper Moco Moco Creek and Karusu Creek (pl. 31, fig. 2). The trail led along the west bank of Moco Moco Creek for some miles, then crossed the stream near a giant silk-cotton tree containing a nest of a Harpy Eagle. From there the trail was obscure, but it led generally eastward to the summit of a rocky ridge. There a second display ground with actively displaying cocks was discovered at the exact spot where Atti had predicted it would be, although it was three years since he had last visited the arena.

Despite extensive searching of the rocks and caves around this second dance area, no nests were found, but one was discovered in a rocky cave very close to the confluence of the upper Moco Moco and the Karusu.

The third probe was made into the forests lying at the western foot of Mt. Ilamikipang. The trail mouth leading into the forest at this point was about 1 mile northeast of the Chacon farm in the upper Kumu Creek area. It was situated in the forest edge at the foot of a rather steep wooded slope, about 100 yards south of Father's Creek. It followed this creek, mostly on its south bank out of sight of the stream, to an altitude roughly estimated to be about 1500 feet above sea level, and there the creek disappeared into rocks. For the most part this trail, which is probably the same one the Schomburgks used (except at lower elevations, where they apparently walked and climbed through the huge boulders cramming the bed of Father's Creek), is a very old Indian highway over the Kanukus to the Rupununi River. It was along this trail that the Schomburgks discovered the urare plant (*Strychnos toxifera*), one of the most potent of Indian arrow poisons. Our guide, who had learned the location of the deadly vine from some botanists, showed us two plants. Both were found near the headwaters of Father's Creek and just below the point where the trail makes the last crossing of the creek.

The summit of Mt. Ilamikipang (pl. 32, figs. 1, 2), where a third display ground of the Cock-of-the-Rock was discovered, was searched for nests, but none was found. This third display ground was in active use at the time of our three-day visit to the summit proper.

PRIMARY STUDY AREA

THE PRIMARY STUDY AREA (fig. 1) was located at an altitude of about 450 feet on the top of a moderately rounded, forested ridge which sloped downward at a pitch of about 20 per cent. This ridge was one of a number of similar ridges forming the northwest face of the Kanukus between Nappi and Moco Moco creeks. It was in the midst of a study area which was roughly 1 mile square and which contained one small creek, the Ellway or Fly Creek. This tiny stream was apparently at its lowest ebb at the time of our visit. I estimated that it flowed at a rate of about a bucketful in five minutes, but this was sufficient to sustain our encampment, which was situated about an eighth of a mile from the lek area. No other source of water was discovered in this region by the expedition.

The spot within the primary study area

where the ground leks of *Rupicola rupicola* were situated (fig. 3) was relatively flat, free of rocks, and floored with light brown earth. (For a detailed description, see p. 47.) I have called this spot and the vegetation around and above it the main display arena, or the display territory. It extended irregularly along the ridge, which led upward in a southeasterly direction. Both above and below the lek area the ridge became much steeper and much more heavily spotted with rock outcroppings. Some 625 feet southeast of the lek area was a nesting cave of *R. rupicola*.

The vegetational formations over the display arena consisted chiefly of medium to old second-growth trees, with an understory of young saplings (figs. 2, 4). The arena was quite open, with a few small palms, some vines, a few fallen trees, and a few rotting logs. The floor was a solid matting of dead

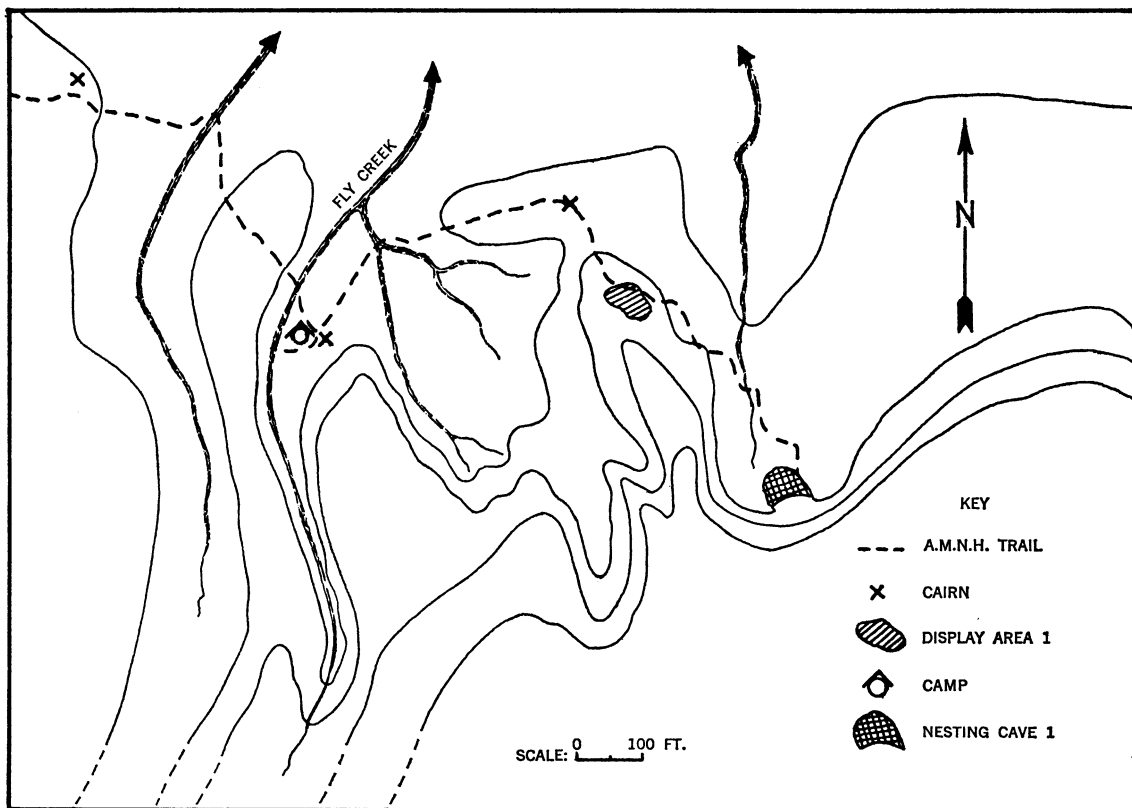


FIG. 1. The primary study area.

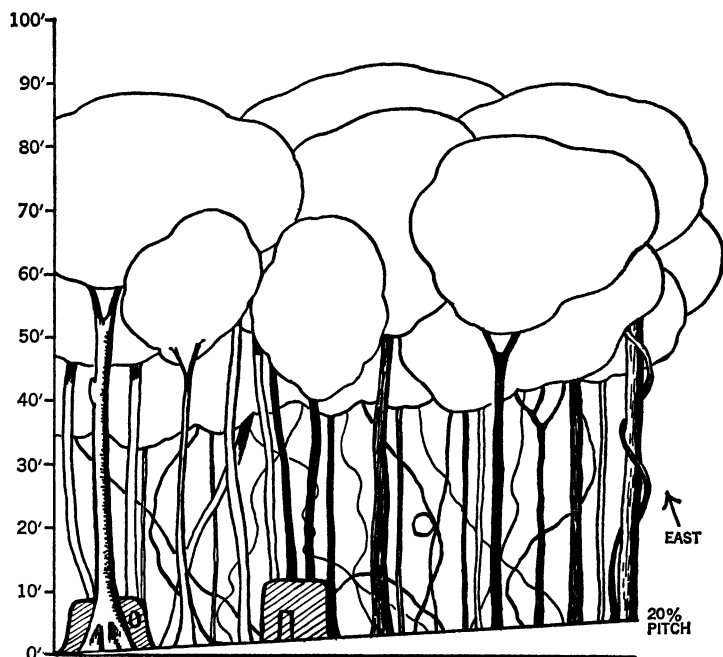


FIG. 2. Profile of large vegetational formations overshadowing display arena.

leaves and fallen sticks, through which earth was visible only in the areas cleared by the cocks. Bordering the display arena and overshadowing its edges was a scattering of about seven original forest trees, the largest of which reached an estimated height of 90 feet. Despite the abundance of fallen leaves, those forming the canopy over the display arena seemed largely intact. We estimated that about 3 per cent of the canopy leaves had been shed, whereas in some neighboring areas a much larger percentage had fallen.

Directly above the leks Roy Hewson and I noticed that the canopy was broken and free of limbs and leaves, and that this opening permitted an unusual amount of light from the sky to penetrate to the forest floor.

The visibility through the lower stratifications of the forest (the slender, second-growth trees and other vegetational formations ranging up to about 15 feet in height) was remarkably good. We estimated that we were able to scan the forest floor for distances of up to 200 feet in some directions, particularly toward the north, where the substage of the forest appeared blighted. In this quarter Hewson and I estimated that 40 per

cent of all the trees less than 15 feet tall had dropped their leaves. This gave the forest substage the open appearance of a New England maple forest in late autumn.

This remarkable openness was due, of course, to regular seasonal changes in the weather. These conditions are normal for the cool, dry season when winds blow almost continuously from the northeast and when, for months at a time, virtually no rain falls and the forests become tinder dry and subject to devastation by fire.

During our 20 days of observations in this forest, the aforementioned conditions of visibility continued to improve as leaves dropped owing to the dryness and the effect of buffeting by the winds. By the end of February the forest had become a dangerous firetrap, and animal life in general, particularly insectivorous and nectar-feeding birds, had virtually disappeared from the display area.

From Indian sources I learned that the forest over and around the display area, and in fact virtually all the forests of the western ramparts of the Kanuku Mountains, are periodically burned as a result of fires started by man in the savannas. Every few years, I

was informed, such fires invade the true forests. The vegetation in the main study area was last burned in 1958. Every decade or so the fires burn to the summits of the range. The presence of the aforementioned second-growth forest, together with an occasional carbon-scarred tree and fallen tree trunks, even on the summit of Mt. Ilamikipang, attested to the authenticity of these reports.

In and about the immediate vicinity of the main display arena we observed a small number of predators, including several species of hawks. One of these was the Black-and-White Hawk (*Leucopternis albicollis*), which often perched in the middle limbs of tall trees near the edge of the display area. Another predator was the ocelot (*Felis pardalis*), which was once observed on a sloping limb not more than 6 feet above the display leks. Curiously, no large snakes or lizards were observed on the display grounds. The tracks of a jaguar (*Felis onca*) were found some 625 feet from the displaying grounds (in the nesting cave of the Cock-of-the-Rock).

The main display arena was casually visited by a small number of birds during the period of our observations. Included were many species of the high and middle strata of the forest, such as macaws, Black and Yellow Trogons, Purple-throated Fruit Crows, barbets, Blue Tanagers, Gray Screaming Pihas, Red-necked Woodpeckers. The ground and low tree trunks were visited by a few ant birds, including the Black-throated Ant Bird (*Formicarius colma*) and a few species of dendrocolaptids, but on the whole the number of bird species observed in the

display area was remarkably small, and hummingbirds were completely absent. This scarcity of birds reflected the ecological conditions described above.

However, over and around the main display arena a number of mammals were observed, including the Guiana squirrel (*Sciurus aestuans*), the large red deer (*Mazama* sp.), and the agouti (*Dasyprocta aguti*), in addition to a number of unidentified species of bats, one of which was almost certainly a vampire bat. No monkey was seen over the main display arena, although the red howlers (*Mycetes seniculus*) were abundant a half-mile distant.

The agouti seemed to enjoy a special relationship with the cocks. I suspect that this dog-sized mammal acts as a sentinel for the cocks and, in return, derives some service from its use of the display lek clearings. This suspicion is supported by Macusi lore and by the discovery of the golden and brown hairs of the lower back of the agouti on some of the lek clearings. Additional support is the following eyewitness account of the shooting of an agouti in a lek area when many cocks were present. Atti said that while hunting near the summit of a range behind Moco Moco he had heard a concentration of displaying Cocks-of-the-Rock. He therefore sneaked up to the crest, and there he observed an agouti with many Cocks-of-the-Rock around it. Atti then shot the agouti. Three years later he took me to this same spot via a long-unused trail. We found there the display clearings and Cocks-of-the-Rock in trees over the clearings. We also found an abundance of the long back hairs of the agouti on the clear earth of the leks.

THE DISPLAY TERRITORY

THE DEFENDED TERRITORY

NO ARTIFACTS were used as aids in determining the extent of the defended territory. However, from prolonged observations of the interactions of a group of wild males, I was able to determine with considerable certainty the approximate limits of the main display arena.

Some of the key observations follow: Groups of displaying males habitually left their "privately owned" ground leks or their "privately owned" low perches, even when in the midst of their displays, to "greet" a visiting male cock. The "greeting" areas were always in what appeared to be the periphery

of the main display arena. Three males, which the writer was able to recognize individually by their special mannerisms, went as a group day after day to greet a fourth male and several times a fifth when the latter arrived at the periphery of the displaying area. In fact, this greeting was a customary late-afternoon performance. The actions of the males that I call combative display behavior (see p. 53) often developed at this time into rather violent fighting displays. The effect of these displays was to prevent the fourth and fifth males from crossing the periphery into the main display arena except for very brief intervals.

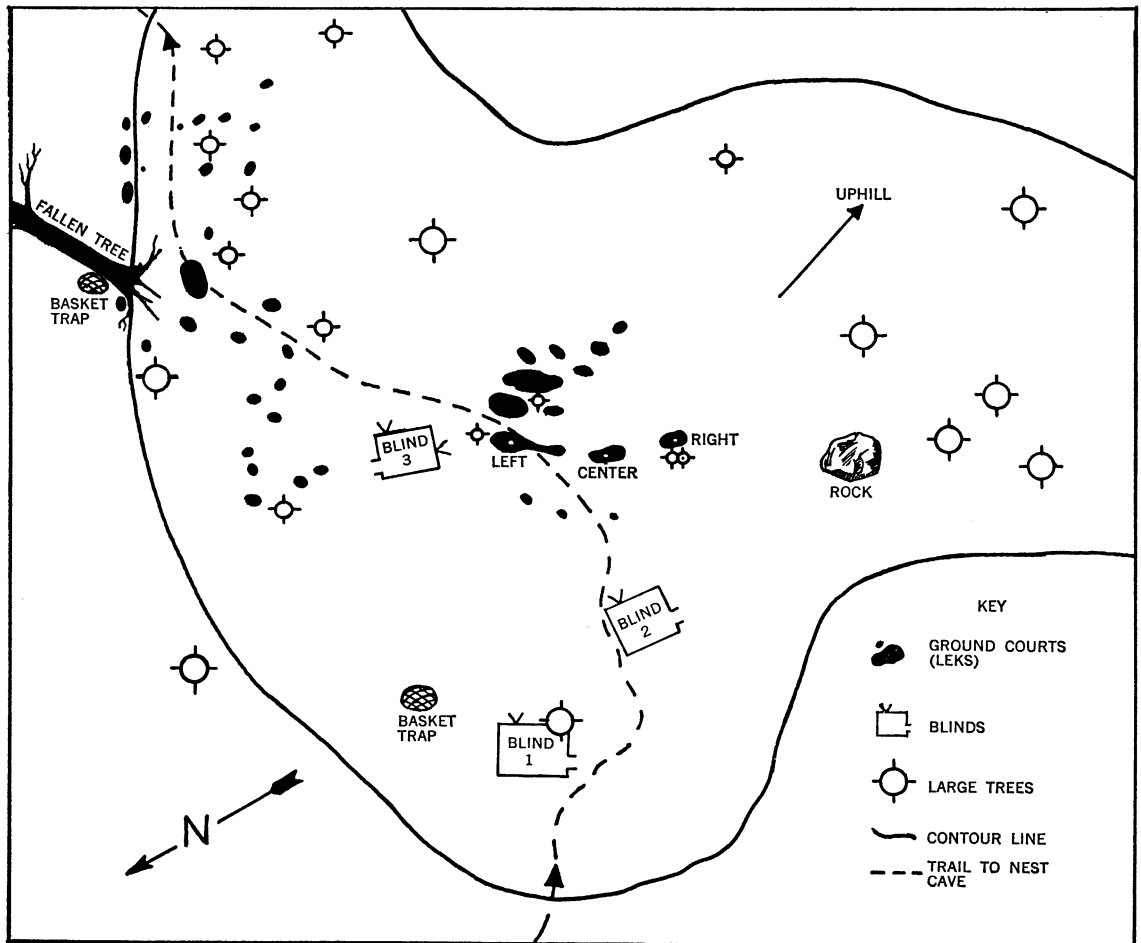


FIG. 3. Ground courts, or leks, of display arena 1.

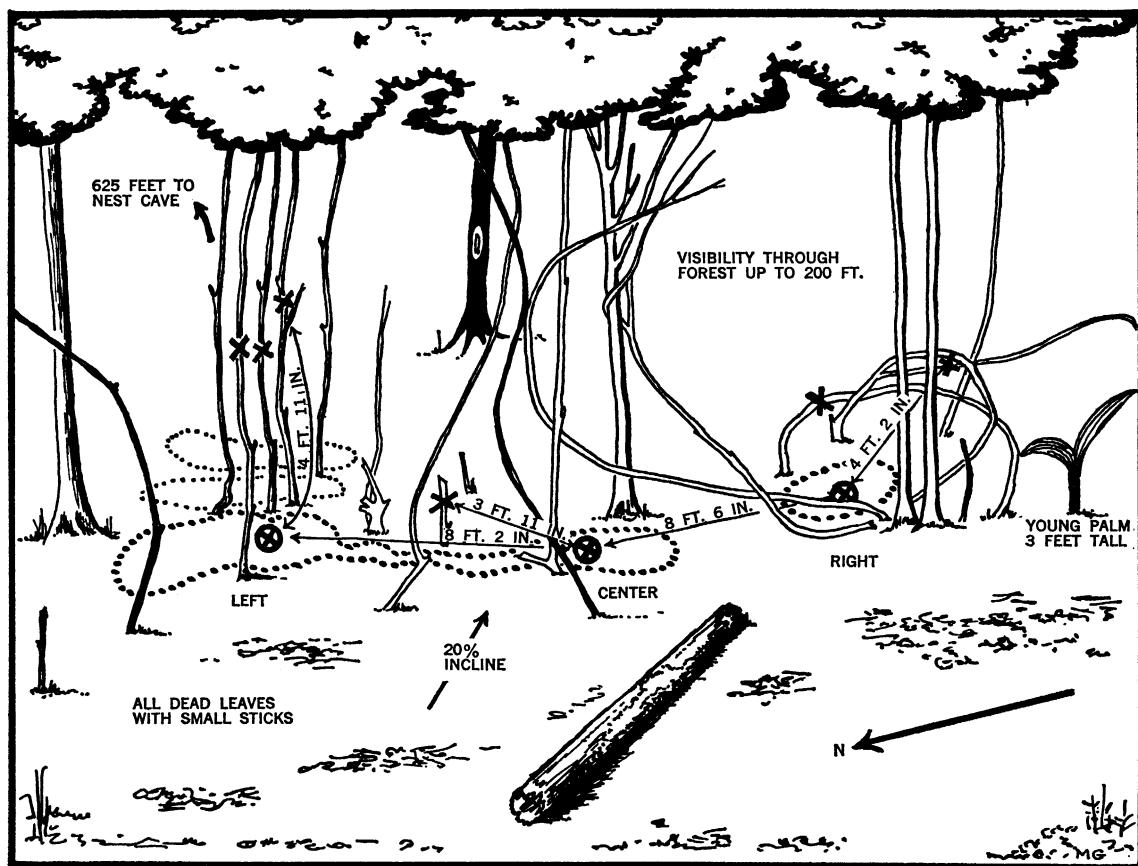


FIG. 4. Cluster of leks in display arena 1.

The territory thus defended was a roughly long-oval space about 40 by 70 feet in diameter. It extended to the sides of the rounded ridge and upward to the small crown limbs just under the canopy of the forest 40 feet up. The focal points within this territory were the terrestrial dancing stages, or leks. The leks were approximately 40 small clearings on the otherwise leaf-covered forest floor (fig. 3). Many of these seemed to be arranged in three ill-defined clusters. The larger leks seemed to be located more or less at the center of the clusters. The locations of the individual stages seemed to be governed somewhat by the distribution of thin saplings and vines which served as approach perches. Only one cluster of leks was in use during the period of my observations (see fig. 4). But this group was in constant use, and the leks were relatively free of fallen debris. At the edge of each lek in this cluster a slender sapling or vine, or

a crisscross of small saplings, was located. The leks varied from about 1 foot to about 5 feet in diameter. The largest leks tended to be oval or rectangular. The small leks were generally round. Some of the leks were floored with cleared earth, but some of the smallest clearings, although free of fallen sticks and leaves, were nevertheless rather solidly floored with a thick mat of small rootlets. Most of the smallest leks were located near the periphery of the display territory, and from this observation I hazard the guess that they are the leks of younger males.

In the leks shown in figure 4, three males habitually visited "privately owned" leks. Their approach perches and actions in general were such that, as mentioned above, I could recognize them individually within the display territory. These birds were identified in my notes as *Left*, *Center*, and *Right*. These designations were also given to the leks used

by the birds (see fig. 4). The leks were located in a line running nearly north and south across the ridge and directly under the above-mentioned opening in the forest canopy. The terrestrial lek where *Left* usually displayed was 8 feet 2 inches from the lek occupied by *Center* (pl. 33, fig. 2), while the lek occupied by *Right* was 8 feet 6 inches away from that of *Center*. *Left* "owned" by far the largest lek, *Center* "owned" the next largest, and *Right* "owned" by far the smallest. However, *Left* was the least active bird (and perhaps the oldest), *Center* was the dominant bird and seemed to be the initiator of the displays, while *Right* seemed sexually the most active, because it was usually the first of the group to begin posturing on the ground and the last to leave its lek.

PRIMARY DISPLAY STAGES OF INDIVIDUAL MALE

No hint that the individual cocks defended their own territories had been given in earlier observations, so it came as a distinct surprise to find that each male habitually displayed only on its own ground clearing. The extent of the defended area of these ground clearings, which I consider to be the primary display stages, was ascertained by my observing the actions of the males on the rare occasions when they had to defend their leks. The key observations follow:

1. One male (*Center*), which was quietly standing on its lek, suddenly attacked another (*Right*?) on a bit of cleared ground near the lek "owned" by *Right*. The cock being attacked then flew off.

2. On another occasion *Center* flew up from the ground to attack a starling-sized bird that happened to fly through the display area as the males were displaying on the ground. This attack occurred 8 to 10 feet almost directly above the central lek. It was punctuated by flailing wings and the sound of thuds as one of the birds was struck by the other. The intruder then flew out of sight.

3. On still another occasion a group of about seven Cocks-of-the-Rock in female plumage (young males?) harassed the displaying males as they stood on their individual leks. The visitors repeatedly flew in and perched on low limbs around the adult

males. When they perched less than 6 to 8 feet from a displaying cock they were immediately attacked. I observed these attacks to defend the lek eight to 10 times. They were of short duration, and the adult cock broke off the attack about 8 feet from its lek, turned, and dived directly back to its private display stage on the ground. On one occasion I observed two cocks attacking intruders at almost the same instant, then they turned and almost simultaneously returned to the leks from which they had rocketed into the air. The intruders seemed to know the limits of the defended areas, because they landed almost immediately after the attack ceased. Although they were safe on perches 12 to 20 feet from the defended leks, they began working their way back toward the peripheries of the leks almost as soon as the "owner" cocks had returned to their property.

On the basis of these observations, it appears to me that the size of the territory "owned" by a cock is usually somewhat greater than the diameter of the lek clearing. As a guess, I would say that it is an area 5 to 8 feet in diameter, with its center being the position on the ground where the male usually postures. The size of the lek clearing may thus serve as an index to the length of its occupancy by an owner and possibly to his age. Old birds may have large leks which are cleared to an average diameter of about 5 feet. Young cocks which have only recently been accepted in the hierarchy of the flock may occupy ground clearings that are very small, perhaps less than a foot in diameter, but I would expect the young male to defend a larger portion of the uncleared ground around his lek than does the old male on the large ground clearing.

Vertically, the defended area may extend upward 8 to 15 feet in a kind of "cone" over each "privately owned" lek. In this "cone" are found the "privately owned" display perches that the individual cocks use periodically for display purposes when they leave the ground, also many of the private approach perches used in the arrival at and departure from the lek area.

SECONDARY DISPLAY STAGES

The series of secondary display perches are

those within the aforementioned "cone," on which the "owner" male perches with his display plumage expanded but which are rarely frequented by other males; and the neighboring unoccupied ground leks, which are occasionally visited by the "owner" cocks but not used when the female or females are present.

The three males, *Left*, *Center*, and *Right*, not infrequently resorted to arboreal perches when they were fully stimulated and their ornamental plumage was fully expanded (pl. 29). These perches are marked with an X on figure 4. Evidently considerable individual variation in habits existed among the three males. *Left* frequently displayed on three vertical shafts averaging some 52 inches above its ground lek (pl. 34, fig. 3). *Center* frequently left its ground lek to display on a short stake 47 inches distant, and, in fact, several times it remained displaying on this stake (pl. 34, fig. 4) a short while after a female had arrived in the display arena, a time when the males usually leaped to the ground. *Right*, however, although it used two perches some 50 inches from its very small earth lek, displayed but rarely except on the ground. But on the ground this male displayed with much patience (pl. 30).

The other secondary display stages were two terrestrial leks which were used but rarely. *Left* occasionally half-jumped and half-flew to an alternate lek (see fig. 4) some 6 feet to the east, and not infrequently *Center* made

short visits to the ground almost under its favorite stake perch.

The males, on their secondary arboreal display perches, habitually sat in very precise positions. Time after time, day after day, their feet were placed in almost precisely the same spot, a fact that was brought home to me while I waited for the birds to perch in a new position if an intervening leaf or branch partially obscured them in my telephoto lenses. I learned that the only course was to move the camera or the obstruction.

TERTIARY DISPLAY STAGES

The tertiary stages were in the dome and the periphery of the display arena. Here the males vied with one another and with visiting males. They often showed certain aspects of their plumage that were not seen at other times, but they seemed rarely to visit the tertiary stages while the ornamental display plumage was expanded. These perching areas were 10 to 90 feet up, and they may serve as waiting stages, under the conditions described below.

WAITING STAGES

These were the perches in the dome and the peripheral crown limbs where solitary males sat while awaiting the arrival of a second male or other males. These perches were 8 to 40 feet up, in some cases above the display area, but in most instances in the periphery of the display territory among the leaves.

THE STUDY POPULATION

ALTHOUGH I DID NOT MARK any birds, for the reasons stated above I could recognize the three adult males, *Left*, *Center* and *Right*, whenever they were in the display territory. The fourth and fifth males were rather frequent visitors. Although I never saw more than five fully adult males together, I once observed a nearly adult male which had much dark brown in the orange-red plumage. It perched quietly for a long time 3 to 6 feet from an adult that I believe was *Left*. I therefore know of only six males (five adults and one subadult) that visited the display territory during my period of observation.

On one occasion (see above) I saw seven birds dressed in female plumage which seemed not to act like females and may have been an itinerant band of young males. The females were very hard to observe, because they perched quietly and were the color of a dark forest shadow. Many times my Macusi Indian sentinel informed me that a female was present in the canopy over my blind, but usually I was unable to confirm his observation. Eventually, however, I observed and photographed a female at the display grounds, then a pair of females at the display grounds, and finally a female as she selected a displaying male.

The primary study population consisted of about five adult males, one nearly adult male, an undetermined number of young males in female plumage, and about seven females.

DISPLAY PARAPHERNALIA

The special body ornaments in the male are the crest, the modified inner secondaries, the highly modified rump feathers and upper tail coverts, the broad white primary barring, and the brilliant orange-red coloration of the plumage, the irides, and the feet.

The crest is permanently erect. It conceals the bill and resembles a Roman helmet. It is composed of two fan-like courses of feathers which spring from the anterior sides of the crown. The two courses are pressed back to back, forming a blade-like crest that is round and subterminally edged with reddish brown. This crest extends forward several millimeters beyond the tip of the maxilla and

conceals the entire bill except for the base of the mandible (pl. 34, fig. 4). The crest serves to exaggerate the visual effect of a pronounced rapid movement used in the inter-male greeting, namely, the bobbing of the head. This ceremony, as I observed it in the field, was as follows: The male suddenly hopped (or stretched its legs) upward a fraction of an inch; at the same time the neck and head were thrust outward and upward and then pulled sharply down to the level of the perch or slightly below it. Then, without a pause, the head was rapidly jerked upward, and the "chopping" action came to a halt at the top of the arc. The ball-like crest moved down and up, down and up, as though it were on a stick hinged to the shoulders of the male. The movement was exaggerated by the position of the "ball" far forward on the bill. A sharp mechanical snap of the bill (see below) accompanied this action.

The modified inner five secondaries (fig. 5B), with their highly fragmented elongated outer barbs, draw attention to the male when he is engaged in his static posture displays. The long, stringy barbs, which extend outward from the sides of the bird, seem to be constantly in motion, even in very light eddies of air (pl. 34, fig. 3). They also serve to embellish wing and body shuffling and shaking—actions that are rather frequent, as in the birds of paradise.

The most prominent plumage signal of the courtship display is the fanning of the upper tail coverts (pl. 38, fig. 1). This is generally done on the lek, as is described below, but also occasionally on the secondary display perches. To exaggerate the motion of fanning or opening the plumage, the upper tail coverts have become elongated, with the individual plumes reaching 55 mm. in length and extending backward over the tail for five-eighths of its length (a typical male had the tail coverts 53 mm. long and the tail 84 mm. long). Also the individual feathers of the upper tail coverts are abruptly broader at their tips (fig. 5A) and even slightly forked, so that, when the "fan" is opened, it does not split up into "spokes." The cock often held



Rupicola rupicola. Left, an adult male, immediately after a long period of terrestrial display



Rupicola rupicola. Three cocks on and over their leks in display arena 1. *Right* (left of photograph) is posturing on ground. *Center* (at right of photograph) is on its private "cut perch." *Left* (top center of photograph) is in subcanopy above its lek



1. View southeast from near mouth of Menari Creek (foreground) toward Kanuku Mountains. Mt. Ilamikipang is just to the left of center in background
2. View southeast into Kanuku Mountains from near confluence of Moco Moco and Karusu creeks. Silk-cotton tree at right; native garden in foreground



1



2

1. Telephoto (300 mm.) of northwest face of Mt. Ilamikipang. In the summit forest, directly behind summit cliff, *Rupicola rupicola* display arena 3 was discovered

2. View northwest from summit of Mt. Ilamikipang. White spot in center background is the Takutu River at Lethem. Area beyond river is Brazilian territory; other areas are British Guiana territory



1



2

1. Blind 2 at west edge of *Rupicola rupicola* display arena 1
2. Lek of cock called *Center* in interacting group of three males found in display arena 1. Note "cut perch" at left where this cock habitually perched



1



2



3



4

1. Cocks assembling in the subcanopy of the forest above the leks of display arena 1
2. Cocks in same area of subcanopy begin their combative displays
3. *Left* on one of its private vertical approach perches above its lek
4. *Center* on its "cut perch" beside its lek. Cock is posturing statically with bill directed backward over shoulder; frequently crest is held parallel to ground



Center posturing on its lek



Centurus posturing statically on its lek. Such positions are often held in silence for many minutes. Movements made to adopt new postures are executed very slowly

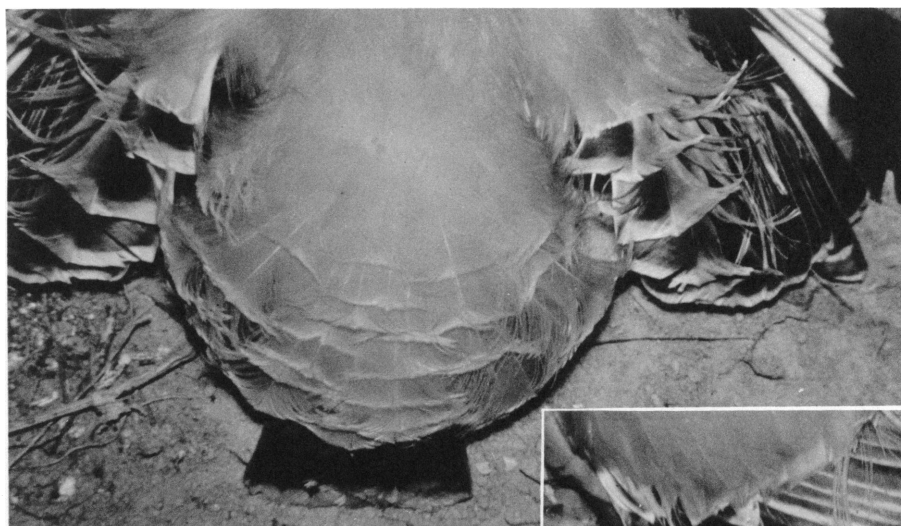


1



2

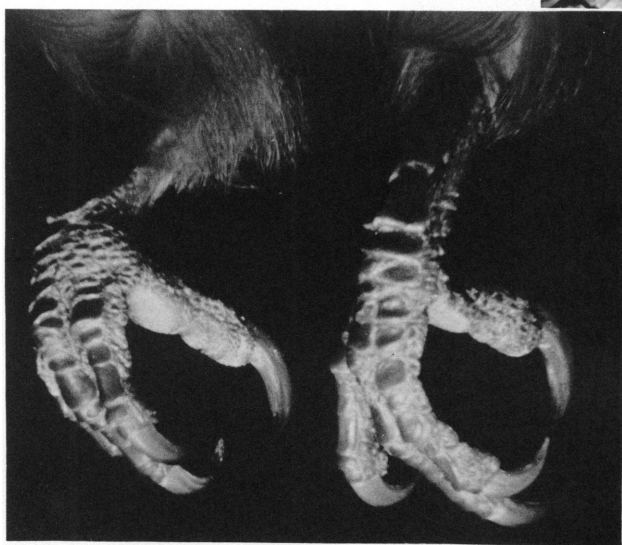
1. Nest 4, with female *Rupicola rupicola* in nocturnal resting position on lip of nest
2. Nesting cave 1 of *Rupicola rupicola*. Nest 3 was plastered to vertical rock face in dark niche directly above head of central figure



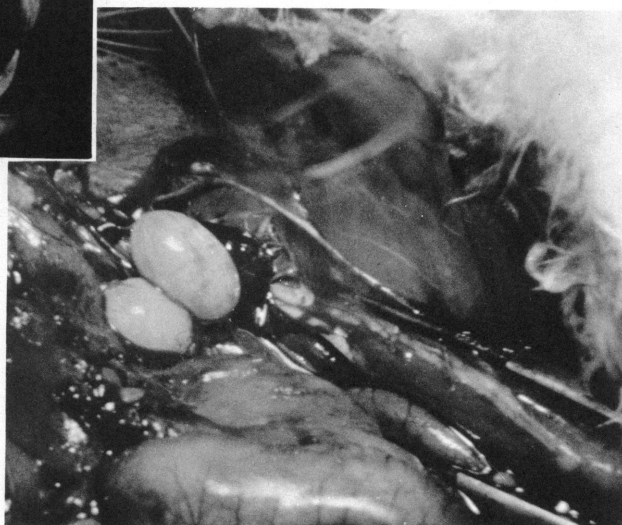
1



2



3



4

1. *Left* immediately after death, showing relationship of ornamental plumage to tail and wings. Cock is shown on its lek
2. *Left* immediately after death, showing whistle-producing spike tip of the second primary (counting from outside)
3. Feet of *Left* immediately after death. Note powerful toes and long nails
4. Testes of *Left*. Tips of dividers are set at 10 mm. This male was the least active of the three interacting cocks



FIG. 5. A. Upper tail covert of *Rupicola rupicola*. B. Innermost secondary of *Rupicola rupicola*. Both $\times 1$.

its shoulders low during the feather fanning, so that the upper tail coverts, when expanded upward, were nearly level with the upper back of the bird, and when the head and crest were held in a canted position the whole upper side of the bird resembled a fan-like ornament nearly parallel to the ground. When elevated and fanned, the upper tail coverts often overhung the wings. In this position they intermingled with the constantly moving outer edges of the inner secondaries, thus adding a moving fringe to the highly unusual ornamental feather fan. During this performance the tail was bent so sharply downward that it often touched the ground, and it was thus out of sight and under the fan, as were the bulk of the secondaries and most of the primaries.

The white primary barring forms a broad speculum when the wings are held partly open, which occurred only in the display fighting and "greeting" ceremonies between males.

ORANGE-RED COLORATION OF THE COCK

When a shaft of sunlight pierced its lek, the cock moved in such a way that its whole body, not certain parts, must be considered

as an ornament. Again and again I noted that the "owner" male became restless in the trees when the sun struck its lek, and then it often descended to the ground. Or, if it was already on the lek, it shifted its whole body so as to be in the sunlight. The shifting light in the forest plays queer tricks on the human observer. At times shafts of sunlight made the males appear golden orange, again in the shadows they seemed dull brownish red, but occasionally the light was such that they were as brilliant as the reddest race of *R. peruviana*.

THE BOWER AS COMPONENT OF DISPLAY PARAPHERNALIA

Because, in a number of the lek-displaying birds, the ground stage, and stage building, have become important factors in the display (and seem to have replaced the function of ornamental sexual plumage in some of the bowerbirds), the lek is included here as a component in the display paraphernalia in *R. rupicola*. In the Cock-of-the-Rock the lek is quite variable in size and shape. The 40 or so bowers that were examined in the primary study area varied from clearings no larger than a dinner plate to several that measured

4 by 6 feet. All the older bowers had been cleared down to the bare earth (pl. 33, fig. 2), but of course many were marred by a superficial covering of fallen sticks and leaves at the time of my visit. The leks that were in use were fairly clear. To my surprise, however, I never observed an "owner" cock to touch anything with its bill or to make any motion other than with the wings to remove debris. Bower building and maintenance therefore seemed to be done solely by blasts of air resulting from the occasional violent jumping of the birds as they stood on their bowers, or by their violent wing braking as they dove into the clearings or took off from them.

I saw nothing to indicate that the bower is an ornament of any importance in the display; nevertheless, I suspect that it does play (or eventually will play) an important part in framing the stimulus situation to which the female responds.

COMPONENTS OF THE DISPLAY

Four types of display are found in *R. rupicola*: vocal displays, which are relatively unimportant; mechanical noise displays, which are important; movement displays, which are important; and static terrestrial displays, which are very important. A résumé of these displays, with notes on their frequency and variability, follows.

VOCAL DISPLAY BY MALES: A composite call, which I have named the "assembly call," was infrequently emitted by a solitary male when it was about to enter the unoccupied arena, or shortly after it had arrived in the arena crown and had found it to be unoccupied by other cocks. This call was generally a loud, bugle-like "ka-waooh" or "kahaaow," which was sometimes uttered twice or even three times in quick succession. The cry was penetrating and carried far through the forest. It seemed to me rather similar to some of the bugled caws uttered by *Paradisaea apoda* under similar circumstances.

Other sounds uttered by the cocks are single "keeow" and "waaow" notes, which were emitted at long intervals by solitary males either when they approached the display arena or after they had been perched

alone for some time in the canopy of the display arena. Still another call was a sharp squawk which was an alarm call. On the one occasion when I clearly witnessed its effects, it caused all the cocks to flee from the display arena. I had been watching three males displaying on and near the ground when the squawk was heard (it was probably emitted by one of the males). Within a matter of a second or two the males had sprung into the air and deserted the arena. They did not "explode" in several directions, but all flew downhill together through the substage of the forest.

Other sounds emitted by displaying males were low, wavering caws and muted, gabbling, fowl-like chatter. These sounds were always produced in an almost continuous stream when the males were interacting combatively in the display arena before or after a period of static displaying on their leks.

One of the most significant features of the terrestrial displays of the cocks is that, from the moment of their landing on the leks, they were silent, and either their movements were very slow and deliberate or the birds were quite motionless (pl. 36). Such silence and slowness, or lack of motion, together with some of the peculiar crouching postures, reminded me very strongly of the nest behavior of passerine birds. Only when a male jumped from its lek at another cock nearby on the ground was there any noise. At such times a single loud squawk was heard as the two birds came together.

VOCAL DISPLAY BY FEMALES: The female, I believe, emits a plaintive "kiuouu" (or "kawee") note. When this rather high-pitched call was given, the males immediately descended to the ground to begin their static displays. The aforementioned band of birds in female plumage, which I believe was an itinerant band of young males, had a call that I wrote as "kawee."

MECHANICAL NOISE DISPLAYS BY MALES: Two types of mechanical noises were emitted by the males. The most frequently heard and the loudest was a snapping noise very similar to that produced by many manakins. The snap closely resembles the sound made by the snapping of thumb and forefinger. It was produced by the snapping shut of the bill at the instant when the head was bobbed. So

fast were the opening and shutting of the bill, and so completely was the bill concealed by the forepart of the crest, that it was virtually impossible to see how the sound was produced. I determined the origin of the sound by snapping shut the bill of a freshly collected male, which produced a snapping sound rather like that produced by the live male.

The snap was produced by the male as a preliminary to social display, usually when a second male or more males came to the display arena in response to an assembly call. When a second male arrived, the solitary male stood up, stretched, and shortly began the bowing, snapping movements and sounds described above. The males then moved close together and proceeded to stimulate one another with this sequence of movements and mechanical sounds.

Near the end of these interactions, or after a session of static displaying, or during the course of greeting a strange male at the periphery of the display arena, a second type of mechanical sound was often heard. This was produced with the wings as follows: The tenth primary (second from the outside; see fig. 6) is modified so that the outer 20 to 25 mm. is very narrow and stiff. With this instrument the male produced a low, undulating sound (a kind of whinnying whistle) whenever it flew. This sound was enhanced by the increased wing activities of the males as they indulged in social chasing and combative activities.

MOVEMENT DISPLAYS: When the solitary male was joined by a second male or more males in the canopy of the display arena, it immediately adopted a display attitude. The key features of this display were the head-bobbing and snapping described above and the posture. The bird stood high on its perch

and soon shifted position so that the males were clustered in a knot; the interacting males were usually 2 to 3 feet apart but sometimes were as much as 8 feet apart. Some yawning, some head flicking, and occasional stretching occurred at this time. The males made sudden little hops toward and away from one another as they executed the bow-snap. Wing flicks immediately preceded each short hop. The tail may be fanned wide as the interactions increase in tempo and the birds tend to crowd together, but the wings are held an inch or so out from the body.

Combative display behavior usually followed which is highly stimulating to the males (pl. 34, fig. 2). The key features of this activity were the almost continuous low notes, the wavering whistles, the partially opened, drooped wings with the white speculum exposed, the violent chasing and fleeing, and the actual physical contact as the combatants struck one another from time to time. These movements were always executed arboreally, either directly over or on the periphery of the display arena.

When the males dove downward, they hovered for a moment just before their feet touched the ground. The white linings of their wings showed during this maneuver, and the fallen debris on the lek was blasted away by the generated air currents. Some males went directly from the canopy to the ground in a steep dive; others, by stages. A typical approach was the following:

Center, which had been on its lek for some time, flew to a perch some 6 feet above the ground; after a moment or two it returned to its usual display perch 47 inches north of its lek. A few seconds later it executed several wing flicks and bob-snaps, then made a jump flight to within 6 inches of the center of its



FIG. 6. Tenth and eleventh primaries of *Rupicola rupicola*. $\times 1$.

lek. Its attitude changed immediately after landing (see below).

STATIC TERRESTRIAL DISPLAYS: As soon as *Center* reached the ground, it froze in an alert position, with its head erect (pl. 36). For perhaps 20 seconds the bird remained quite still, then it gave a wing flick and jumped 6 inches to the center of the lek. There, while standing high on its legs, it elevated the rear of its body, slowly opened its upper tail coverts, tilted its head and slowly elevated its back so that its entire upper side was more or less parallel to the ground (pl. 35). It then remained completely stationary for many minutes.

Although such was the basic display posture on the ground, there were occasional variations. A favorite attitude was that of a stationary barnyard rooster, with the chest puffed upward and outward, the back sloping downward. The bird stood high on its legs, with its broad orange shanks sticking down like posts to the tarsometatarsus flat on the ground. The crest was directed upward, and the rump feathers and upper tail coverts flared sharply outward from the steep line of the back.

After holding this position for some four minutes, the bird suddenly hopped and then assumed the symbolic nesting posture (see pl. 36 and p. 52). Stooping, as if it were about to lower its breast onto a nest, the male crouched for a few seconds, with its upper tail coverts widely fanned, and then began to turn its head very slowly.

HEAD-TILTING POSTURE: In this posture the male appeared to be observing the upper part of the forest (pl. 35). The head was slowly tilted to the side so that either the left or the right eye looked nearly straight upward. This pose was held for a minute or even longer. The act was often performed in the symbolic nesting posture, with the back nearly parallel to the ground.

HEAD-OVER-SHOULDER POSTURE: In this position, which in some cases was held for many minutes, the head was very gradually tilted about 125 degrees over the left shoulder (pl. 35), and the crest and cranium were tilted forward so that the right eye was directed upward and the left eye toward the ground. At other times the head was turned

backward so the right eye was aimed into the plumage of the back and the left eye looked obliquely upward toward the front. The head-tilting and head-over-shoulder postures were the most common terrestrial postures, and they were also assumed on the private display perches above the leks.

EYE-CATCHING MOVEMENTS ASSOCIATED WITH STATIC POSTURES: Although these postures were silent and relatively static, they incorporated certain movements which seemed designed to attract attention. The most vivid of these was a single stiff-legged hop. This usually carried the cock an inch or two upward, after which it generally settled back on the same lek. This sudden motion, I believe, served as a means of drawing attention to that spot of gold on the forest floor where there was a cluster of similar, static spots of color.

The second movement was more subtle. The fragmented, elongated barbs of the inner secondaries tended to hang in a fringe of feathery golden tassels along the sides of the displaying male. They are so light that they are easily agitated by the slightest puff of air, and as a result they are in almost constant motion, which catches the eye of the human observer, at least (pl. 35).

Variations were frequent. After periods of terrestrial posturing, some of the males, particularly *Left* and *Center*, flew up to their arboreal display perches, where they continued to tilt the head, fan the upper tail coverts, and assume contorted postures, including the head-over-shoulder position (pl. 34, fig. 4). In addition to this arboreal perching, the males often seemed to hang in awkward poses as if they were sick or in a trance. Toward the end of the active display, either on the ground or in trees, the black primaries were suddenly unfurled and then closed over the still-expanded plumage of the lower back. This changed the cock's appearance completely.

ANNUAL PERIODICITY AND DAILY RHYTHM OF DISPLAY

The only data that I have on the periodicity of display I obtained from Atti, who reported two periods of near maximum display in *R. rupicola*, one about Christmas and the

other at Easter. During my observations (February 7 through February 26) there was a slight waning of the display activities, but the same three birds occupied the same leks and display perches every day at about the same times. Furthermore, there was no decrease in the number of visits paid by itinerant males, one or two of which called at the periphery of the display arena almost every day, usually in the late afternoon.

At about 7.30 A.M. (when my observations began), occasionally one, usually two, or very often three males were to be found in the display arena. They were so constantly in attendance that I suspected that they must sleep there, but two night searches failed to prove or disprove this. The greatest average activity occurred between 1.00 and 2.00 P.M., when almost every day the males descended to their ground leks to posture. At other periods of the day they visited the leks many times, but the least activity was in the morning before the sun had penetrated to the forest floor. At this time the males were usually absent.

EFFECTS OF WEATHER

Only once during the bright part of the day did I observe the males to desert the display arena and its periphery of trees completely. On this occasion it was at least 10 and probably 20 minutes before the first cock flew back and gave an assembly call. Wind and overcast weather tend to thwart display, but the birds remained in or around the arena even when heavy winds were blowing and sunlight was absent. Sunlight stimulated display, and when a ray of sunlight reached the leks the birds became excited and tended to move toward it. I once observed a male that was frozen on its lek move about a foot to freeze again in a shaft of sunlight. I do not know what effect rain has on the displaying birds because I experienced no rain with the exception of two very short sprinkles.

INTERACTIONS AMONG ADULT MALES

Interaction began at about 7.30 A.M., when the first cock usually returned from feeding to the display arena. As it approached, it emitted several loud assembly calls. It then perched very quietly in a slumped position

some 40 feet up among the concealing leaves of the peripheral canopy. A second male usually arrived within a few minutes. It perched some 6 feet from the first cock (pl. 34, fig. 1), which immediately began bowing and snapping. A third was apt to arrive a minute or two later, and before long all three males were snapping and bowing and perching restlessly 2 to 8 feet apart (pl. 34, fig. 3). As the males became stimulated by their interactions, they moved progressively lower and toward the center of the arena. About five minutes later one of the cocks flew down to a low perch near its lek (pl. 34, fig. 4), and usually the others followed. If they did not, the leader cock made a few intention movements, which suggested that he would go to the ground alone. If they did not follow, he generally returned to the group. Then the snapping and bowing increased in intensity, with some combative chasing interspersed. Soon a second descent began. Often the three males flew or swooped down simultaneously to their individually "owned" displaying perches, where they clung like wrens to vertical saplings (pl. 34, fig. 3) or perched in the normal way on vines and limbs. In a very short time one cock jumped to the ground, where it immediately became virtually motionless and silent (pl. 30). Within a few seconds the others followed, and they too immediately became stationary on their leks (pl. 35). When the three males were on the ground, they often faced in different directions. Occasionally the birds executed a single hop or an upward flutter, the motions involved in assuming new postures, but usually they were motionless on the ground. Once in a while a bird flew up to a low display perch beside his lek, displayed there (pl. 29), and then returned to the ground. At intervals the three cocks flew up to higher perches in the arena where they perched for many minutes, sometimes even for an hour or more, before beginning anew the cycle of snapping and bowing, approaching the ground, and posturing.

Interactions appeared to be most intense in the early afternoon. In the mid and late afternoon the males tended to perch farther from their leks and higher in the trees near the edge of the display arena. Late in the

afternoon they most frequently engaged in combative greeting ceremonies with itinerant males, which seemed prone to call at that time.

INTERACTIONS AMONG MALES AND FEMALES

Six times during the 20 days of my observations I saw a female or several females as they visited the males in the display arena. On six other occasions I knew that a female or several females were in the vicinity, but I failed to see them. Two of my observations were of two females (my identifications are based on mannerisms and plumage and are fairly positive). The remainder were of solitary females, one of which was observed to fly down and select a mate. Copulation was not witnessed.

The visits by a female or several females were most frequently observed in late morning or early afternoon. The males seemed to know many seconds in advance that a female was approaching the display arena. They immediately dropped to their leks, began posturing, and remained there as long as a female was in the vicinity. One female lingered for more than 10 minutes.

On one occasion I observed a female as it perched about 7 feet from the ground and very near my blind. It was on a slender, nearly horizontal branch of a small sapling. Below it, near the foot of the sapling, were the three males, *Left*, *Center*, and *Right*, which had been posturing for more than five minutes when I happened to sight the female through a crack in the blind. It sat on the same perch several minutes longer, then flew down to the lek where *Center* was posturing and hit the ground 3 to 5 inches to the left of the cock, striking with such force that the impact was clearly audible 20 feet away. Without a pause it then flew off like a skipped stone. The male, which had been frozen on its lek, emitted a squawk and pursued the female, so quickly that the birds were only a yard or so apart. *Left* and *Right* then moved slowly, and in a few minutes they jumped up into the low branches over their leks. They made no attempt to join in the chase.

These interactions are probably those that take place immediately prior to copulation. I should be more certain of this, however, if I had not made the following observations of

chases that were somewhat similar but that I am inclined to believe represented an attack on adult cocks by a band of young males.

INTERACTIONS AMONG ADULT AND IMMATURE MALES

I once observed a flock of seven birds in female dress which were quite bold as they flew around and above the displaying cocks, unlike the adult females, which were fairly secretive and hard to observe when they visited the display area. They approached within 10 feet of me crying "kawee, kawee," even though I was standing in an exposed position at the edge of the display arena. This band of birds, I believe, was composed of itinerant young males. It was the only band of its type that I observed during the 20 days I spent in the area. The following description of this event is taken directly from my field ledger:

"About 10.37 A.M., three cocks are 'frozen' on their ground leks. The [young males?] are very noisy; flitting about, crying 'kawee,' they come lower and perch close to the ground near the cocks. A [young male?] seems to attack a 'frozen' cock on the ground. Other [young males?] are calling and shifting positions 4 feet above the posturing cock.

"A cock on the ground, although he appears to be in a trance, suddenly leaps up at a perching [young male?] a few feet above him and violently chases him. Another cock does the same to another [young male?]. There are many 'kawee' notes, now long and drawn out.

"Much action continues to occur. There is never more than a moment of inaction by the group. Cocks bounce up in violent attacks, [young males?] fly off, then return.

"I watch and note again a posturing cock, absolutely frozen, as it suddenly lunges up from its private ground lek at a [young male?] that has perched a few feet above it. This [young male?] shies off to land on a limb 10 feet away and 4 feet up. The cock lands only 4 feet up and 5 feet from its lek. It stays a few seconds, then turns and dives (a gliding dive with violent braking wing-flapping just above the lek) right back to its lek.

"I watch as two cocks, fresh from their upward attacks from the ground, dive back to

the ground after chasing off the [young males?].

"The cocks land almost simultaneously some 8 feet from each other on their own leks and then immediately seem to stoop over and become part of the ground as they adopt postures.

"A [young male?] now flies in and perches 1 foot above a cock. Almost instantly the cock leaps and flies up at it. But he does not follow far, he perches 3 feet up on a low, stake-like perch just above his lek while the [young male?] flies a full 10 feet before perching several feet above the ground. The cock

after about 20 seconds turns and dives back to his ground lek to posture again.

"And so it went, the [young males?] intruding on the territories of the three cocks, the cocks attacking and driving them off from their curious ground stations, then the [young males?] intruding again—all to the frequently executed calls of the [young males?] who called 'kawee' over and over again. At 10.45 the display was suddenly over. At its end the cocks flew up to low perches and, I noted, one was missing from the arena."

THE NESTING TERRITORY

A NESTING CAVE with four nests was discovered some 625 feet east of and slightly (100 feet) higher than the main display arena. This cave, which was situated at the head of a rocky draw, consisted chiefly of a rock, 30 feet high, that had rolled down the mountainside and become lodged in the draw (pl. 37, fig. 2). Ground and stones had piled up behind the rock, but a cave extended under it on the downhill side to the northwest, and on the north side the nearly vertical walls of the great boulder sloped outward to form high, rain-protected overhangs. The nests were located in the cave and under the overhangs. Although an extensive search was made of all the rocks and caves in the vicinity, no trace of additional nests could be found.

Unlike the courtship area, which was under a canopy of tall forest and which had an even flooring of light brown earth, the nesting territory was located in an area about 100 feet in diameter with no forest cover. As a result, the equatorial sun could reach the rock tops and caused a major difference in the ecology of the nesting area. The upper surfaces of the cave rock were very dry, with six tall cactus plants growing upon them. A forest fire had recently killed several large trees on the top; the sides of the rock were bare except for a fringe of large-leaved plants near the upper rim and a very large nest of stingless bees which protruded from the west face. Around the base of the rock on the downhill side was a grove of some 20 tall, slender Congo palm and papaya trees; some of the latter grew within a few feet of the face of the nesting rock.

The discovery of this grove of papayas was a surprise, because they were not to be seen anywhere else in the forest. Their presence probably indicates that the Cock-of-the-Rock raids native gardens in the forest, and that the birds fly considerable distances during the course of their food-getting excursions.

We made about a dozen visits to this nesting area between February 6 and February 26 to study the nests and to check them for eggs. During all the night and most of the day visits, females were observed on and near the

nests. Males, however, were never seen in the vicinity of the nest rock. The females often perched on the edge of the nest. By day they sometimes flew into the cave while we were there but rushed out when they saw us. At other times, even though the nests were without eggs, a female perched silently but nervously in the forest edge 30 feet from the rock face during our inspection of the area. At night both new and old nests, the latter being little more than fragments of mud bases, were used as perching areas each by a single female. I estimated that the study population of females consisted of at least four birds, but that there may have been as many as eight.

On each of our six night visits we found one to three females perched on the rims of as many nests. We were thus able to determine that each of the four nests was the sleeping place of a female. Photographs were made of the females on these perches (pl. 37, fig. 1). At first the birds were hard to approach. Not only were they very wary, but they seemed able to see well enough to fly at night. During our first attempts we felt our way in virtual blackness over the rocks to the nest positions and then made flash photographs from memory. This method did not work very well because the females flushed if we made the slightest sound. Finally I discovered that I could pin the bird on its nest for a minute or so by flashing a flash bulb, but, even when temporarily blinded, the female flew if we made any noise.

The specific locations of the nests were as follows:

Nest 1 was outside the entrance of the cave, in bright light on a tiny ledge 9 feet up under a broad overhang of rock. It was an old nest, with the mud base present but the nest cup missing. A female was photographed sleeping on this nest.

Nest 2 was little more than a mud base 9 feet up under an overhanging area of rock. It was on a small ledge in an area of perpetual dryness in moderately good light. An Indian ladder stood against the rock 2 feet to one side of this nest.

Nest 3 appeared to be a new nest. It was

located $7\frac{1}{2}$ feet up inside the cave in an area of deep shadow (pl. 37, fig. 2). It was built of mud against a vertical wall and later was found to weigh $8\frac{1}{2}$ pounds. A tiny drip of water ran out from the inner reaches of the cave. Wet mud in small quantities was available along the edges of this seep. Under this nest were two areas which had been well plastered with orange and yellow droppings and one that was plastered with blue-black droppings. A female was photographed on

this nest.

Nest 4 was 8 feet up on a well-defined ledge of an exterior face of the cliff. It was in a well-shaded, dry area in a chimney between fallen rocks. A small splattering of blackish droppings was under this nest. A female was photographed sleeping on this nest, and on March 29 David Snow found eggs in it. This was an old nest with a dark tan mud base, a new top of reddish mud, and a new cup of rootlets and vines (pl. 37, fig. 1).

SPECIMENS COLLECTED

NEST

NEST 3 WAS COLLECTED and placed in the American Museum of Natural History collection. This nest, which weighs $8\frac{1}{2}$ pounds, is 280 mm. in height, 205 mm. in width, and has a cup 120 mm. in width and 45 mm. in depth. The mud is about as hard as adobe. It is pale pinkish brown, with rootlets and fine vines interspersed through the mud. Around the upper edge a shiny, agglutinative substance resembling hardened saliva acts as a binding agent to hold the edges of the cup in place. The nest is lined with a shallow basket of fine black rootlets of a type that grow commonly on the external surfaces of tree trunks; also included in the nest lining are some brown rootlets and several leaf ribs. This heavy, massive structure was found attached to a vertical and nearly smooth wall in an area that was perpetually dry. The area of the nest that adhered to the rock was 10 inches in height and 8 inches in maximum width.

MALE

On the twentieth day of observations *Left* was collected and preserved in spirits. Immediately after its death, I manually opened and closed the bill. By so doing I was able to produce a somewhat weaker version of the snapping sound made by the cock when it executes the bow-snap. Next a series of color photographs were made (see pl. 38), showing the details of the head, bill, upper tail coverts, the spike-like second primary, the perishable colors of the eye, the feet, and the testes. At this time I made a description of the perishable colors as follows: iris rose-red; outer half of bill yellow; inner half all around rose-red, internal bill parts, both hard and soft, and tongue pale yellow to amber yellow; feet pale rose, with pale rose-yellow to yellow interscutal skin; nails pale

yellow, with blackish outer dorsal ridges and tips.

TESTES CONDITION: The testes were 12.5 by 8 mm. and 10 by 7 mm. They were deep ivory white. (Two photographs in color with divider tips set at 10 mm. next to the testes were made; pl. 38, fig. 4.) The testes were somewhat flaccid and may have been in process of reduction.

MOLT ANALYSIS: A careful molt check revealed that *Left* was in completely fresh dress throughout the wings, tail, and body plumage.

STOMACH CONTENTS: Fruits with small and large (up to 10 mm.) seeds (saved in alcohol). The pulp of these fruits was green; the seeds were irregular in shape and bone-colored.

MEASUREMENTS (IN MM.) IN LIFE: Total length, 303; wing, 180; tail, 86; bill from base, 28; tarsus, 37; crest, 34 from crown between eyes; length of crest from front to back, 70; width of upper tail covert fan when extended, 142 (pl. 38, fig. 1); length of longest plumes in the upper tail covert fan, 73; extension of crest beyond end of bill, 2.

MALLOPHAGA: Before preservation, the male was placed in a transparent, airtight bag, and a fog of Aerosol insect spray was applied. The bird was left in the gas for five minutes; then the insects were shaken out. The plumage, which is white beneath the orange, was then scanned with the aid of forceps, and a few very small insects were recovered. These have not yet been identified.

FOOT STRENGTH: When first winged, the male *Rupicola* seemed about to recover and fly off. I therefore picked it up and was promptly punctured by two of its claws. The bird clasped my hand with almost the strength of a small owl and drove its claws (pl. 38, fig. 3), into the base of my right little finger. I should say that it possessed extraordinary strength for a passerine bird.

COMMENTS ON THE DISPLAY OF *RUPICOLA RUPICOLA*

IN THE PRESENT preliminary study of the arena behavior of *Rupicola rupicola*, I attempt to decipher the sign stimuli that regulate the reproductive cycles that are received from the habitat, the sign stimuli that govern the interactions between the males, and the sign stimuli that govern the interactions between the males and the females.

SIGN STIMULI RECEIVED FROM HABITAT

LIGHT: The cocks were relatively inactive in the duller parts of the day, and they tended to become excited and active when a shaft of sunlight penetrated to their leks, which suggests that light intensity on the floor of the forest may be important in the regulation of the reproductive cycles. The light intensity in the substage of the forest is seasonally very variable in the Kanuku Mountains. During the period of my observations, for example, skylight could penetrate much deeper than at most other seasons of the year because a large proportion of the leaves in the substage had been shed as a result of regular seasonal changes. I suspect that such changes in daylight, which in equatorial birds are, of course, not correlated with changes in day length, are significant as regulators of breeding cycles. Perhaps they act as the triggering agents for the reproductive cycles of many tropical forest birds.

SOUND: The virtual lack of rain during February caused the forest to become tinder dry and very noisy with the rustling of leaves. The fallen leaves were indeed so crisp that predators would have had much less chance of stalking the displaying Cocks-of-the-Rock on their ground leks than at most other seasons of the year.

SIGN STIMULI BETWEEN MALES

The striking transformation that immediately was observed in a solitary male when a second male or several males entered the arena suggests to me that a strong social bond exists between the males of the arena clan—a group bond that is perhaps an outgrowth, or a redirected tendency, of the pair bonds characteristic of phylogenetically less-

advanced passerine birds. Instead of the pair stimulus, males in the group stimulate one another through their bowing and snapping, hopping, wing and head flicking, wing waving, chasing, fighting, wing winnowing, and fowl-like chattering.

A primary function of these inter-male, inter-clan activities is to defend the display arena from penetration by foreign males. The usual manner in which such defense was accomplished was for the lek "owners" (the clan members) to fly in a group to the visiting male as it reached the periphery of the arena and there to engage him in a rather violent session of display fighting, which in effect served as an intimidation display. Probably another function of these inter-male displays is to select the clan members and to establish their position in the hierarchy of the clan. But how this might operate with regard to the distribution of the terrestrial ground clearings within the display arena I do not know. The distribution of the "privately owned" ground leks (with the larger stages tending to be surrounded by smaller ones, and with the latter tending to be closer to the periphery of the display arena) suggests that the stages were of different ages, the small ones being the newest.

Another point to consider is the probability that the biologically most valuable lek locations are near the center of the display arena. This probability is based on the supposition that predation in the display arena is not random but is more severe around its edges, where terrestrial predators would make their first contacts with the displaying cocks. Another fragment of evidence to be taken into consideration is that on the one occasion when I observed a female selecting a mate, she chose the central one of the three males.

SIGN STIMULI RECEIVED BY FEMALE FROM MALE

The sign stimuli that appear to be most important in the selecting of a male by a female are the lek locations and the display posture. When the female came to the arena, she perched 6 or 8 feet up. The males, which

took up their positions on the leks and maintained them in complete silence and with very little movement as long as the female remained in the area, stood out vividly from the brown of the forest floor. The female therefore sees a series of rather similar, gold-colored objects, complete with more or less similar display paraphernalia. She sees the head canting, the head-over-shoulder postures, the crest silhouetting against the lek, the expanded feathering of the lower back and upper tail coverts, the wind-agitated tassels of the inner wings. She notices the occasional hops and the vivid coloration of the cocks, especially when a shaft of sunlight strikes a bird. She sees the variations in display and at length, perhaps after a number of visits, she responds to these stimuli.

SIGN STIMULI RECEIVED BY MALE
FROM FEMALE

Although the male seemed to be in a state of shock when the female was in the display arena, he could probably see her from his lek. If so, he watches as she becomes progressively more agitated, twisting her head back and forth and partly opening her mouth. He may even see her when, on rare occasions, she signals her choice by diving suddenly downward. All the posturing males hear her as she strikes the surface of a lek beside the male, but only the cock the lek of which has been touched follows her as she rushes out of the arena. The rejected males cease displaying and leave their leks for perches in the canopy of the display arena.

EVOLUTION OF ARENA DISPLAYS

TWO QUESTIONS are paramount in any study of arena behavior: What are its biological advantages? How does such a pattern of behavior evolve? The answer of the first question seems, in part, to be that polygynous habits make it possible for a very much smaller percentage of the males of each generation to perpetuate the species. In the Cock-of-the-Rock it is the expendability of the males which, I believe, makes it possible for these non-protectively colored males to invite death by going repeatedly to the ground to perform their courtship displays. But more than that, the higher death rate may be advantageous in that it fosters more rapid selection.

The second question is more difficult to answer. My first hint of how such a pattern of behavior might have evolved in the Cock-of-the-Rock came when I noted the transformation in the cocks at the moment when they arrived on their leks. They acted vaguely as though they had just arrived at their nests, and their subsequent actions were reminiscent of a bird engaged in cautious nest care. Next I noted that there seemed to be a correlation between the colonial group of nests, each "owned" by a female which spent much of her time quietly perched on the rim, and the colonial cluster of ground leks 625 feet away on which the males stood quietly in the semi-static attitude of birds engaged in nest care.

Another hint came when I removed nest 3 from the nest cave. I found that it weighed $8\frac{1}{2}$ pounds, and was largely constructed of droplets of mud, which must have been carried to the nest site by the female. To carry such a quantity of mud, the female must have had to visit the ground many hundreds of times.

It is well known that nest building and the actions associated with it, in this case ground visiting, are deeply seated "fixed action behavioral patterns" which are not easily dropped. Instead they are much more easily diverted and incorporated into new activities. These observations therefore point to the strong possibility that the ground-visiting lek behavior of the Cock-of-the-Rock originated as a displacement activity for nest-building or nest care, or both.

Finally, how could this elaborate pattern of arena behavior have originated from the primitive one that doubtless preceded it? The answer in part may be that the change from monogamous, work-sharing habits to polygynous, non-work-sharing habits evolved by small steps over a long period because some factor of survival directed the behavior toward an unequal division of labor, or possibly two forces were responsible for the shift. There might have been selection for bright plumage in the male (sexual selection) together with selection for greater nest security as expressed in the acquisition of increasingly cryptic plumage in the parent chiefly engaged in tending the nest (natural selection).

In the Cock-of-the-Rock stock I believe natural selection was the primary force that led to the establishment of conditions in which arena behavior became possible. First, the advantage derived from greater nest security shaped the evolution of a stock in which the tendency was for the males more and more to remain separate from the females and the nest. Eventually such separation led to the forming of a species in which monastic groups of males served only as sperm pools. With this advance the second force became dominant and from this threshold onward it seems plausible to postulate that the accession of brighter and brighter sexual ornaments and more and more complicated sexual displays were the result of the process of sexual selection.

With these thoughts in mind, I made a brief survey of arena birds. To qualify as an arena bird, a species must not only maintain a breeding station that is not used as a feeding or nesting area (Mayr, 1935), but it must be polygynous; there must be no pair bond beyond actual mating; the male must take no part in the construction care, or defense of the nest; and the males must display (usually on private courts) within the arena.

Arena birds that have been studied sufficiently well for one to determine whether or not they fit the above criteria are the following: the Ruff (*Philomachus pugnax*), of which the arena is very small and the males

defend leks that are small circles a foot or two apart (the males are as quiet as those of *R. rupicola*); the Prairie Chicken (*Tympanuchus pallidicinctus*), of which the private leks are up to 30 feet in diameter (with their boundaries rather more flexible because the competing cocks frequently cross them when a female visits the arena); the Sage Grouse (*Centrocercus urophasianus*) (Scott, 1942; Simon, 1940), of which the arena may be 200 yards wide and half a mile long and may contain more than 400 cocks each standing 25 to 40 feet apart on private leks, the positions of which signify the hierarchy (and mating privileges) of the clan. Others are the Capercaillie (*Tetrao urogallus*) and the Blackcock (*Lyrurus tetrix*), both of which have private leks ("cantons d'accouplement") within the borders of the arenas which they visit before daybreak (but the Blackcock tends to run after the visiting female with its ornamental plumage expanded rather than to posture stiffly as she approaches, as does the Capercaillie); and the Argus Pheasant (*Argusianus argus*) of which the arena may be a large section of hill forest with individual cocks displaying on 6-foot leks which are located far apart but probably within auditory range of each other and, according to Beebe (1926, p. 188), where the females probably spend several days with the males of their choice before departing to take up the full duties of nest building and the rearing of young.

Among the passerines the following arena birds have been studied: Gould's Manakin (*Manacus vittelinus*) (Chapman 1935), of which the arena is a long, narrow area of forest floor 12 to 200 feet in length and the private leks are small circles of cleared ground about 25 feet to 35 feet apart; the Blue and Red Manakin (*Chiroxiphia pareola*), of which the one arena studied by the author (Gilliard, 1959b) was in a narrow zone of forest 160 feet in length with four leks 45 to 60 feet apart, and with the leks themselves slender vertical and horizontal perches close to the ground; the Bearded Manakin (*Manacus manacus*), of which the arena is a large area of forest, sometimes with large numbers of leks; and Jackson's Dancing Whydah (*Drepanoplectes jacksoni*) (Van Someren in Armstrong, 1947, p. 242), of which the arena

is a territory of grassland containing as many as 100 leks, each consisting of a ring of beaten grass encircling a central tuft. Van Someren informed E. A. Armstrong that the male of Jackson's Dancing Whydah "creates recesses resembling the early stages of a nest, butting into the grass and smoothing it down with his breast." To this Armstrong added, "This performance would seem to be due to the survival of the nest building impulse." The females of this species, like those of the Cock-of-the-Rock, live apart from the polygynous males and breed colonially half a mile or so from the display arena. The Greater Bird of Paradise (*Paradisaea apoda*) of the Aru Islands and the Lesser Bird of Paradise (*P. minor*) are arboreal arena birds, both of which employ small arenas in which private territories, if any, are poorly defined. The arena of the Count Raggi Bird of Paradise (*P. raggiana*) is an area of forest up to 500 feet in diameter in which the males have well-defined, private, arboreal leks. The arena of the King of Saxony Bird of Paradise (*Pteridophora alberti*) is an area of forest a mile or more in diameter, in which individual males have their private leks thousands of yards apart, on limbs high in the canopy. The arena of the Magnificent Bird of Paradise (*Diphyllodes magnificus*) is also a large area of forest, but the males of this species have their private leks thousands of yards apart on the butts of low saplings and on the ground just underneath them. The "privately owned" bowers of Archbold's Bowerbird (*Archboldia papuensis*) are located on the ground under mountain forest in an arena of unknown dimensions. The arena of Lauterbach's Bowerbird (*Chlamydera lauterbachii*) appears to be an area of grassland several miles in diameter, in which individual males build their elaborate bowers hundreds to thousands of yards apart. However, since some much-studied Australian species (see Marshall, 1954) of bowerbirds appear to undergo pair formation, not all bowerbirds can qualify as arena birds, despite the strong probability that the stick bower is an artifact influenced by displacement activities for nest building.

Although, generally speaking, there is an astounding similarity of courtship pattern in these widely different species of arena birds,

the species that appears most similar to the Cock-of-the-Rock in behavior is the Jackson's Dancing Whydah, because the cocks appear to be engaged in nesting activities on their leks and because the females nest socially. It is curiously enlightening that the nest-like actions of the male should have suggested nest behavior to Armstrong. Such also was my impression as I watched the weird postures of the Cocks-of-the-Rock on their courts, and from it stems my belief that arena behavior is largely influenced by displacement activities for nest duties. The many analogies of behavior found in unrelated birds that resort to arena behavior further convince me that arena behavior in general has a common origin—the origin postulated for the Cock-of-the-Rock. In short, arena behavior is courtship behavior as reshaped by emancipated males to include

their non-discardable nesting tendencies.

The special adaptive advantages that accrue from this type of behavior may be associated with an increase in the rate of evolution, because in the practice of promiscuous polygyny only a few males of each generation are required for the species to survive. Such a system, in which predatory loss can be very acute, permits natural selection to operate much more severely, and the same is true of sexual selection. In short, arena behavior must accelerate the processes of evolution, and possibly such acceleration is responsible for the radiation and shaping of the highly specialized combinations of structure and behavior that we know in all arena birds, be they the Argus Pheasant, the Jackson's Dancing Whydah, the birds of paradise, or the Cock-of-the-Rock.

TAXONOMIC CONCLUSIONS AND SUMMARY

AT THE OUTSET of this study, I suspected that the Cock-of-the-Rock was a large, aberrant manakin. Now I believe that the numerous characters that it shares with the manakins (ranging from morphology through mechanical noises and patterns of behavior) are not phylogenetic in origin but are due to convergence. Evidence that weighs very heavily is derived from a study of the nest which is very unlike the nests of manakins. Whereas many manakins suspend a fragile basket from a tree, the cock plasters a large, heavy, saliva-and-mud nest against a vertical cave wall. I have found nothing in the ethology or nest morphology to indicate that the Cock-of-the-Rock is more manakin-like than cotinga-like, and, in my opinion, *Rupicola* is, as has long been believed, closer to *Procnias*.

SUMMARY

Ethological observations of the breeding behavior of the Cock-of-the-Rock as observed in 1961 in the mountain forest of the Kanuku Mountains, British Guiana, are reported. Three dancing arenas were studied. At one, observations were made over a period of 20 consecutive days. The behavior of the cocks in their display arena is described, and their display attitudes and their display paraphernalia are illustrated. It was found that a clan of three cocks, each with its own terrestrial lek, joined forces to defend a social display arena some 70 feet in diameter in the mountain forest. The clan males lived in and around this arena almost continuously. The females lived apart from the males in the vicinity of a nesting cave 625 feet from the display arena. In this cave were four nests on which the females habitually slept and on which they often perched by day.

The interactions between adult males, between adult males and a wandering clan of young males, and between the adult males and females are described. The adult males posture stiffly on their ground leks when a female visits the arena. They resemble bits of gold carpet on the brown floor of the forest. The manner in which the female signals a prospective mate is described. A general description

of the ecology and meteorology of the Kanuku Mountains precedes a discussion of arena behavior in general. In the latter are comments on the biological advantages of this form of breeding behavior, and its probable mode of evolution. The advantages are postulated as resulting from the greater expendability of the males (a much smaller percentage of each generation is needed for the perpetuation of the species), permitting more severe selection and consequently more rapid evolutionary advancement. Arena behavior in the Cock-of-the-Rock is postulated as having arisen as a fortuitous result of the division of work between the sexes. This division is postulated as having resulted from two forces that may have been working simultaneously: natural selection in the direction of cryptic coloration in the parent attending the nest, and sexual selection in the direction of brighter plumage and conspicuous patterns of behavior in the male. The peculiar stationary terrestrial postures of the males on their private leks are thought to have resulted in part from relict tendencies (displacement activities) for nest building and nest care. These tendencies are postulated as having been superimposed on the pattern of courtship. The nests are built of mud droplets gathered by the female. One nest weighed $8\frac{1}{2}$ pounds. The carrying of this amount of mud must have required many hundreds of visits to the ground by the female. Therefore ground visiting (like nest building) is believed to be a deep-seated activity, a fixed action pattern, of the central nervous system which is far more easily diverted than dropped, which is an added reason for assuming that lek building and arena behavior evolved largely as displacement activities for nest building and nest care—activities that doubtless were once components of the behavior of the males of the primitive cotinga from which the Cock-of-the-Rock originated.

An outline of arena behavior throughout the world is given. The hypothesis is advanced that arena behavior has a common origin in all the birds that practice it. It is courtship behavior as reshaped by emanci-

pated males to include their non-discardable nesting tendencies, as is postulated for the Cock-of-the-Rock.

The taxonomic conclusion is reached that, despite its manakin-like ethology, *Rupicola* is probably closely allied to *Procnias*.

BIBLIOGRAPHY

- ARMSTRONG, EDWARD A.
1947. Bird display and behavior. New York, Oxford University Press, pp. 1-431.
- BEEBE, WILLIAM
1926. Pheasants, their lives and homes. New York, Doubleday, Page and Company, New York, vol. 2, pp. 1-309.
- BERGER, A. J.
1961. Bird study. New York, John Wiley and Sons, Inc., chap. 5, pp. 130-161.
- CHAPMAN, F. M.
1935. The courtship of Gould's Manakin (*Manacus vitellinus vitellinus*) on Barro Colorado Island, Canal Zone. Bull. Amer. Mus. Nat. Hist., vol. 68, pp. 471-525.
- FOX, H. M., AND G. VEVERS
1960. The nature of animal colors. New York, the Macmillan Co., pp. 1-246.
- FROST, W.
1910. The Cock of the Rock. Avic. Mag., ser. 3, no. 1, pp. 319-324.
- GILLIARD, E. T.
1959a. The courtship behavior of Sanford's Bowerbird (*Archboldia sanfordi*). Amer. Mus. Novitates, no. 1935, pp. 1-18.
1959b. Notes on the courtship behavior of the Blue-backed Manakin (*Chiroxiphia pareola*). *Ibid.*, no. 1942, pp. 1-19.
1962. Strange courtship of the Cock-of-the-Rock. Natl. Geogr., vol. 121, no. 1, pp. 134-140.
- DARWIN, CHARLES
1871. The descent of man, and selection in relation to sex. New York, D. Appleton and Co., vol. 2, pp. 1-409.
- GUPPY, N.
1958. Wai-wai. New York, E. P. Dutton and Co., Inc., pp. 1-373.
- HARRISON, C. J. D.
1961. Display from a captive Cock-of-the-Rock. Avic. Mag., vol. 67, no. 3, pp. 102-106.
- HINDE, R. A.
1956. The biological significance of the territories of birds. Ibis, vol. 98, pp. 340-369.
1959. Behavior and speciation in birds and lower vertebrates. Biol. Rev., vol. 34, pp. 85-128.
- HINDE, R. A., AND N. TINBERGEN
1958. The comparative study of species-specific behavior. In Roe, A., and G. G. Simpson (eds.), Behavior and evolution. New Haven, Yale University Press, chap. 12, pp. 251-268.
- KENDEIGH, S. C.
1952. Parental care and its evolution in birds. Biol. Monogr., vol. 22, nos. 1-3, pp. 1-358.
- MARSHALL, A. J.
1954. Bower-Birds, their displays and breeding cycles. New York, Oxford University Press, pp. 1-208.
- MAYR, E.
1935. Bernard Altum and the territory theory. Proc. Linnean Soc., New York, nos. 45, 46, pp. 24-38.
- MOYNIHAN, M.
1955a. Remarks on the original sources of displays. Auk, vol. 72, pp. 240-246.
1955b. Types of hostile display. *Ibid.*, vol. 72, pp. 247-259.
- SCHOMBURGK, RICHARD
1922. Richard Schomburgk's travels in British Guiana 1840-1844, Leipzig, 1847. Translated by Walter E. Roth. Georgetown, British Guiana, "Daily Chronicle" Office, vol. 1, chaps. 8 and 9, pp. 300-368.
- SCHOMBURGK, ROBERT H.
1841a. Report on the third expedition into the interior of Guayana, comprising the journey to the sources of the Essequibo, to the Carumá Mountains, and to Fort San Joaquim on the Rio Branco, in 1837-38. Jour. Roy. Soc. London, vol. 10, pp. 159-190.
1841b. Journey from Fort San Joaquim on the Rio Branco to Roraima, and thence by the rivers Parima and Merewari to Esmeralda on the Orinoco, in 1838-39. *Ibid.*, vol. 10, pp. 191-247.
1841c. Journey from Esmeralda on the Orinoco to San Carlos and Moura on the Rio Negro, and thence by Fort San Joaquim to Demerara, in the spring of 1839. *Ibid.*, vol. 10, pp. 248-267.
- SCOTT, J. W.
1942. Mating behavior of the Sage Grouse. Auk, vol. 59, no. 4, pp. 477-498.

- SIMON, J. R.
1940. Mating performance of the Sage Grouse. *Auk*, vol. 57, no. 4, pp. 467-471.
- TINBERGEN, N.
1952. "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. *Quart. Rev. Biol.*, vol. 27, no. 1, pp. 1-32.
1956. Social behavior in animals. London, Methuen and Co., Ltd., pp. 1-150.
1960. Behavior, systematics and natural selection. *In* Tax, Sol (ed.), *Evolution after Darwin: The evolution of life*. Chicago, University of Chicago Press, vol. 1, pp. 595-613.
- VAN TYNE, J., AND A. J. BERGER
1959. Fundamentals of ornithology. New York, John Wiley and Sons, Inc., pp. 1-624.
- WHITE, REV. W. G.
1917. Notes from the hinterland of Guiana. *In* Beebe, W. G., I. Hartley, and P. G. Howes, *Tropical wild life in British Guiana*. New York, New York Zoological Society, vol. 1, chap. 34, pp. 453-487.

