

A Lek's Icon

The courtship display of a Guianan Cock-of-the-Rock

Famous for their fabulous plumage but little studied, the unique breeding behavior of this most spectacular cotinga is revealed for the first time

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THE COTINGAS comprise a family of neotropical birds whose members include some of the most beautiful, most grotesque, most behaviorally bizarre birds in the world (Snow, 1982). Like Howard Hughes and Greta Garbo, many cotingas enjoy a paradoxical notoriety: they are famous, but mysterious. Family members include the Amazonian Umbrellabird (*Cephalopterus ornatus*), whose gleaming black pompadour makes it one of the world's most extravagantly ornamented birds, and the White Bellbird (*Procnias alba*), which produces, gram for gram, the loudest bird sound in the world. Although familiar to ornithologists everywhere, they remain little-studied. Threatened by the devastation of their rain forest habitat, these and other wonderfully-named cotingas such as the Screaming Piha (*Lipaugus vociferans*), the Bare-necked Fruitcrow (*Gymnoderus foetidus*), and the Handsome Fruit-eater (*Pipreola formosa*), may never receive detailed scientific investigation.

The most spectacular member of this spectacular family is the Guianan Cock-of-the-Rock (*Rupicola rupicola*). Fluor-

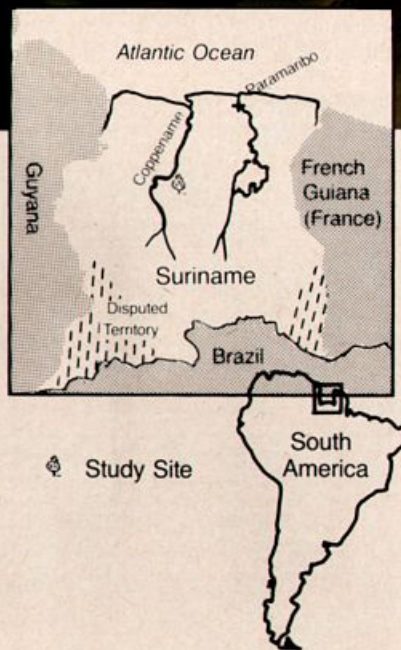


Figure 1. The Guianan Cock-of-the-Rock feeds mostly on fruit high in the tree-tops of neotropical forests. They also consume insects and lizards. So where's the beak?

scent one can barely convince oneself that one is looking at a bird at all (Figure 1). Field studies conducted over the past five years at the Raleigh Falls-Voltzberg Nature Reserve in Suriname, South America, reveal that the mating behavior of the Guianan Cock-of-the-Rock is as elaborate as its plumage.

The male Guianan Cock-of-the-Rock is neither involved in any aspect of nesting or parental care nor does it so much as defend food sources or nest sites with or for females. Instead, males spend virtually all of their time in courtship display. This courtship is highly social, being conducted at a dense aggregation of displaying males called a lek. The clustered

rescent-orange males are bedecked from their helmet-like crests to their ballooning puff of ruff feathers with an impressive array of display plumes. At first



Figure 2. The fluorescent orange males with their brilliant helmet-like crests almost glow in the greenish jungle gloom. Nearly all male lek species have striking adornments or unusual adaptations used solely to signal females. Males typically remain perched above their courts until the arrival of a female at the lek.

males glowing orange in the shadowy green light of the rain forest is a dazzling and unforgettable sight (Figure 2).

Although the social organization of males on the lek may appear chaotic, it is, in fact, rigidly structured. Each male defends his own small display territory (Trail, 1985A). The display area is centered on a cleared "court" on the forest floor (Figure 3). These courts rarely measure more than 1-2 meters wide and include the adjacent defended perches. They contain no food or other resources needed by females. The species' lek serves simply as the rendezvous where the sexes meet and mate.

Following mating, females nest unaided and, except for random encounters at the fruit trees where both sexes feed, they do not interact with males again until their next breeding attempt. Nests are placed in rocky areas where caves and clefts provide shelter for the massive mud constructions (Figures 4 and 5). Protected from the weather, these nests are reused from year-to-year. Any necessary repairs are made by the female with mud and vegetable fibers in the weeks prior to breeding (Figure 6).

Not until this study was the complete sequence of courtship behavior in the Guianan Cock-of-the-Rock known. Tantalizing fragmentary descriptions had, however, been previously published (Gilliard, 1962, Snow, 1971). The following account is based on more than 24 months of field work over five breeding seasons at a lek that averaged 55 territori-

al males per year. During this time, more than 3500 courtship sequences and 400 matings were observed. With a single exception, all matings were performed by individually color-banded males, and in approximately one-third of the cases, the female was banded as well.

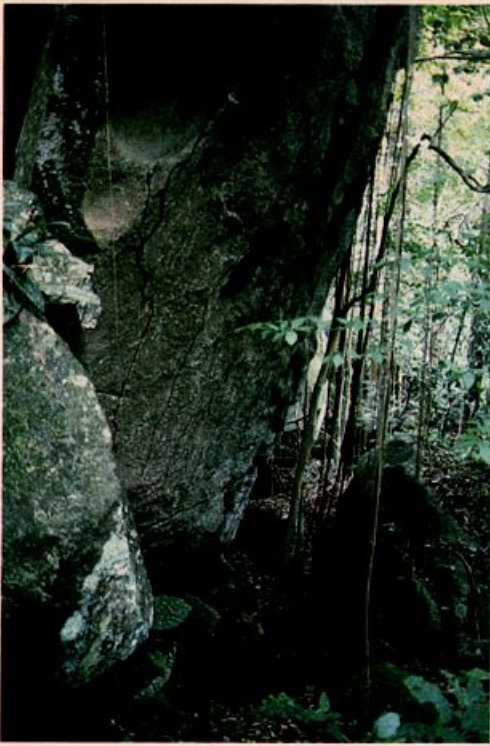
Like other birds with lek mating systems, such as the Sage Grouse (*Centrocercus urophasianus*) (Wiley, 1973), and the White-bearded Manakin (*Manacus manacus*) (Lill, 1974), the Guianan Cock-of-the-Rock is highly polygynous.



Figure 3. Upon arrival of the female, the male Guianan Cock-of-the-Rock lands on his court with a loud squawk and begins his greeting display — violently beating his wings and emitting resounding raucous calls.

Certain males in the display group attract and successfully mate with females, whereas others fail completely. In 1981, for example, 61 males defended display territories at the lek, but only 26, or 43%, performed matings, while the top male accounted for 30% of matings all by himself (Figure 7). Why certain males are preferred remains unknown. Observations of marked (color-banded) individuals reveals that courtship in the Guianan Cock-of-the-Rock involves a prolonged process of sampling potential mates by females. In the Voltzberg study population, the typical hen Guianan Cock-of-the-Rock visited the lek on six days. During this time she visited three different males a total of nine times, but usually mated with only one.

THE FEMALE GUIANAN Cock-of-the-Rock approaches the lek in the leafy subcanopy of the forest, 10 or more meters up, where her dark brown plumage hides her in the jungle gloom (Figure 8). The males are continually alert for female arrival and respond to it with a spectacular "greeting display," which is also usually the first sign to a field observer that a female has entered the lek. The normally silent males burst into ringing choruses of raucous, crowing calls and drop from their resting perches (1-2 meters from the ground) down onto their courts. After hitting the ground with a thump, each male stands erect and violently beats his wings, flashing the dramatic, usually concealed, black and white primary



Figures 4 and 5. The author (bottom of photos) provides the scale by which to measure the cliff face. Nests are concealed in or on rock clefts and in high caves, where they are protected from the weather and reusable from year-to-year. The cock-of-the-rock is a somewhat social nester so that sometimes nests are built within a few yards of each other on the same rock face.

feathers (Figures 9 and 10). In addition to being a real show-stopper, this wing-beating blows loose debris from the court, clearing the surface for the coming display bout. The greeting display may involve a series of one or more flights between perches and the ground, accompanied by wing-beating and loud chorusing. This vocalization is audible for 100-200 meters. Additional females often arrive within the next few minutes.

The pandemonium of the greeting display usually lasts from one to five minutes, although it may continue much longer early in the breeding season or when a large group of females (four or more) arrives simultaneously. As the violent activity dies down, females move to low perches close to the males' ground courts. Now the males assume the static, crouched posture of full courtship display. From perches 2-6 meters up, the female Guianan Cocks-of-the-Rock are able to survey the display of many of the densely-clustered males simultaneously, without "committing themselves" by entering an individual male's territory. The ease of such scanning may be an important benefit gained by the females of lek-breeding species. Scanning is energy efficient as it eliminates the need to travel between widely-spaced males before selecting a mate.

Eventually, often after repeated chases by both territorial and non-territorial males, the hen moves low enough to enter the defended territory of a specific

male. She lands on one of his defended perches, 1.5 meters or less above the ground, thereby initiating a courtship visit (Figures 11 and 12). She has, at least temporarily, restricted her courtship sampling to a particular male by entering his breeding territory.

The subdued nature of the Guianan Cock-of-the-Rock pre-copulation period contrasts sharply with the wild calling and wing-beating of the greeting display. Males hunker down on their courts, crouch low on their tarsi, and often rest their chests on the ground. The male's display plumage erects to its greatest ex-

tent: the crest fully expands, the chest thrusts out, the filamentous fringes on the secondary wing coverts deploy, and the puff of rump feathers fluffs out into a soft and inviting cushion. An important feature of this display is that the male keeps his back turned to the female at all times. This presents his wing fringe feathers and rump puff to their best advantage. The male remains silent and motionless in this posture, only occasionally giving short vertical hops, rapid glances back at the female, and brief muttered grunts when the tension becomes unbearable.

From her low "stand-off" position, the



Figure 6. The massive mud and vegetable fiber construction holds a clutch of one or two eggs. These are a pale brown or buff ground color with lilac-gray blotches and spots overlaid with olive brown.

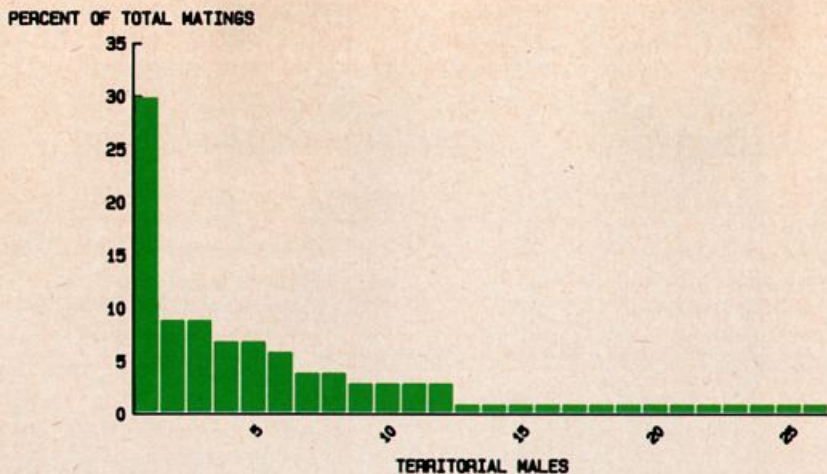


Figure 7. Mating distribution at the Voltzberg study lek, 1981. The bars represent the percent of total matings ($N=138$ matings) performed by each territorial male on the lek ($N=61$ males). Thirty-five territorial males (57%) did not mate at all in 1981. And one male was responsible for an astounding 30% of all matings.

female may now hop down onto the court itself, initiating a ground visit and creating the opportunity for close-range interactions with the displaying male (Figure 13). Ground visits vary in duration from little more than a second to more than two minutes, although visits longer than 30-40 seconds are unusual. Since the displaying male is already facing away from the female, she typically lands behind him. If she happens to land in front of him or to the side, he quickly swivels to face away again. If possible, he erects his plumage still further and maintains his posture even more rigidly (Figure 14).

This new, pre-copulatory phase of courtship usually involves a fascinating physical probing of male by female. She hops warily forward and touches the motionless male, either resting her chest in the pillow of his rump ruff or pecking at his rump and wing fringe feathers. The

exact function of this oddly-touching tactile perception is uncertain. Does it test the male's ability to maintain his rigid display posture? Does it enable a female to overcome her intimidation or fear of the normally aggressive male? Or does it signal the male that the female is ready to mate? This physical contact between the male and female before mating appears to synchronize the pair for copulation. However, it is not always required: a significant number of matings occur without any preliminary touching.

During her presence on a male's territory, a female performs a series of short ground visits, hopping back and forth between stand-off perches and the court.

DURING 10% OF ALL courtship episodes, complications are introduced by the bumbling arrival of a year-old male cock-of-the-rock. These typically



Figure 8. Hidden in the jungle canopy, the female is able to survey the densely clustered males before selecting an individual male.



Figure 9. During the greeting display, a male cock-of-the-rock may fly back and forth between one of his defended perches and the ground several times.

adolescent yearlings are blotchy in appearance, awkward, and erratic in behavior (Figure 15). Although they never attempt to defend display territories, yearlings regularly practice courtship behavior, sometimes toward females, but even more frequently toward crouching adult males. They even mount adult males (Figure 16), who are remarkably tolerant of the yearlings, possibly owing to the strong selection pressure on males to maintain the rigid courtship crouch.



Figure 10. The black and white primary feathers, hardly evident when the male is at rest, add even more flamboyance to the males' greeting display. The violent wing-beating also serves to blow loose debris from the court. Pepper M. Trail, copyright © National Geographic Society



Figure 11. The female may visit several males at the lek, but usually mates with only one.

The yearlings' misdirected courtship behavior frequently disrupts, and occasionally even terminates, female courtship with a particular male. Courtship visits are also frequently disrupted by threat displays, displacements, or direct attacks on the female (or the displaying male) by adult males, in most cases territorial neighbors (Trail, 1985B).

If these disruptions are avoided, or at least contained, pre-copulatory interactions between the male and female continue. After a female has remained on his court for longer than 15-20 seconds, the male usually begins to make small hops,



Figure 12. A female initiates a courtship visit by landing on a defended perch. The males in the immediate area of the arena respond by turning their backs and crouching in a rigid display posture. In contrast to the greeting display, males will remain almost silent and motionless throughout this phase of courtship.



Figure 13. A female pays a ground visit to a particular male. In response, he erects his plumage still further and maintains his rigid posture facing away from her.

glancing over his back at her. Because he is facing away from the female, the male must circle completely around in order to mount, and the female often flushes during the male's approach. These attempted mounts and other pre-copulatory behaviors stimulate nearby males to beat their wings and give distinctive screaming vocalizations, the "copulation alert call." These piercing calls appear to be threat behaviors, sometimes flushing the female from the court, and functioning as a low risk means of interfering with the final courtship stages. If the female remains on the court despite the hops and short feints of her male and the calls and wing-beating of his neighbors, she is probably ready for copulation.

The female Guianan Cock-of-the-Rock must cooperate for copulation to occur. When males attempt forced copulation with visiting females, seizing and grappling with them while attempting to mount, the females always struggle vio-

lently, breaking free within a few seconds. The female Guianan Cock-of-the-Rock is quite capable of avoiding unsolicited matings, thereby exercising control over her choice of a mate.

Copulation usually occurs on the court itself (Figure 17), although it may take place at a low stand-off perch. Mating typically lasts 10-15 seconds, and is consummated with vigorous wing-beating and thrusting by the male. It is accompanied by the shrill chorus of "copulation alert calls" from the mating male's neighbors, which may attract the attention of other females in the area, and unquestionably attracts the attention of the researcher. The female usually terminates the mating by hopping out from beneath the male and moving to a stand-off perch to preen. About one-half of the females return for a second mating before laying their one or two egg clutches, typically returning to the same male unless their first mating was disrupted.



Figure 14. During a ground visit, the female may peck at the motionless male's wing fringe or rest her chest in his rump ruff. What purpose this serves is not clear, and copulation often occurs without this preliminary touching.



Figure 15 (left). Though bumbling male yearlings have no lek territory of their own, they frequently disrupt the lek and add to the general chaos by practicing courtship behavior.

Figure 16 (above). Older male cock-of-the-rock are remarkably tolerant of the yearlings, who, confused, often mount males as well as females in their attempts to mate.

Once females lay their eggs, they do not return to the lek until they are ready for another nesting attempt. Meanwhile, the males continue their display, ceaselessly advertising for sexual partners.

As far as is known, the social complexity of the courtship of the Guianan Cock-of-the-Rock is the most extreme of any cotinga. Even the closely-related Andean Cock-of-the-Rock (*Rupicola peruviana*), does not form such large leks and does not seem to have so rich a pre-copulatory display (Snow, 1982). However, our knowledge is still scanty. Surely the courtship of such spectacular, sexually dimorphic species as the Long-wattled Umbrellabird (*Cephalopterus pendu-*

liger), the Crimson Fruitcrow (*Haematerus militaris*), and the Purple-breasted Cotinga (*Cotinga cotinga*) are fascinating, but they await study.

The cotingas are primarily fruit-eaters and are dependent upon large areas of undisturbed jungle in which to forage. Neotropical forests are especially vulnerable to man's accelerating destruction. With the large-scale alteration of these forests, the ancestral display arenas of these and other neotropical lekking species are threatened. Without vast neotropical forest habitat, the beauty and intricacies of these species' courtship would pass away, never again to astonish and delight us.



Figure 17. Mating lasts about 10 to 15 seconds and usually occurs on the ground. About 50% of the females return to mate for a second time with the same male before laying their clutches.

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